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SEASONAL MOVEMENTS AND THE OSMOTIC BEHAVIOUR OF THE SHRIMP, CRANGON CRANGON L.

BY

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INTRODUCTION

The original object of this investigation was to determine the main factors governing the distribution of the common shrimp (*Crangon crangon* L.) in Dutch waters.

A detailed study of this distribution (prior to the closure of the Zuyderzee) was published by Havinga in 1930. The main results of this investigation are:

Towards autumn most of the shrimps leave the Dutch shallows (Wadden) for the North Sea. During spring and early summer an invasion of the brackish waters takes place. The shrimps then penetrate into what was formerly the Zuyderzee and into the estuaries of the Scheldt.

This short account gives only a schematic picture of the actual course of events. In reality it is more complicated owing to the different behaviour of males and females and of the younger and older stages. As a large part of the experimental work to be recorded in this paper is based upon the data procured by Havinga it is necessary to give a more detailed account of his results.

The data were obtained by continuous examination (during a period of about two years) of the occurrence, number and size of shrimps in the former Zuyderzee, the Scheldt estuaries, and the adjoining shallows and coastal regions. The area of investigation is divided by Havinga into four natural zones (fig. 1), each characterized by different conditions as to the composition of the population and to propagation. The following summary is almost literally quoted from Havinga's publication.

From December until March zones III and IV are almost

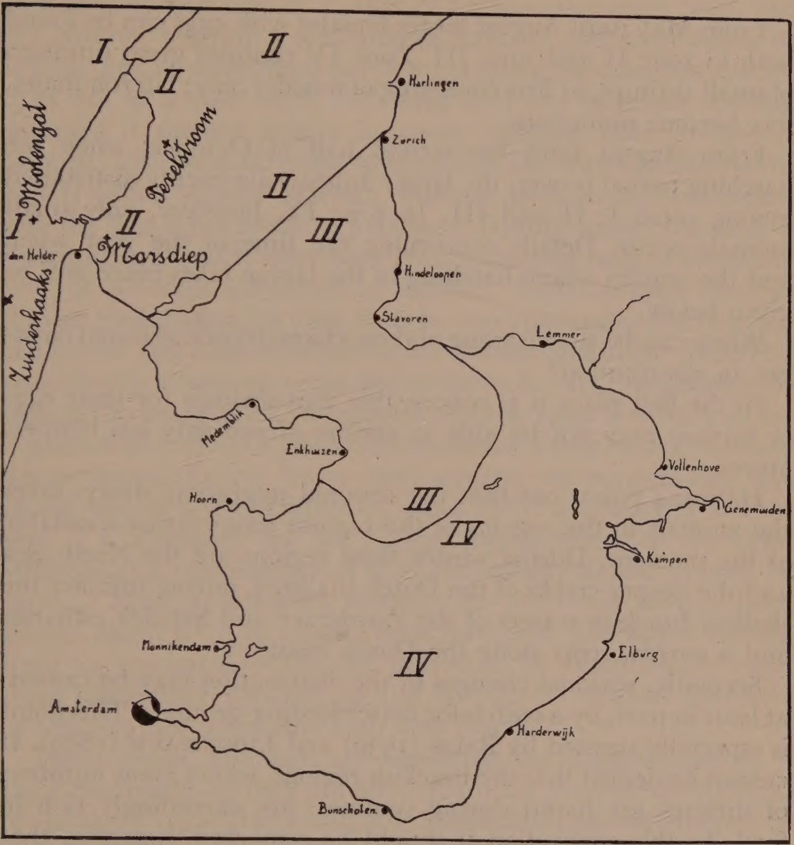

Fig. 1. (After Havinga, 1930)

abandoned. In zone II mainly young animals remain (males as well as females). Zone I contains the older females (both with and without eggs) and the older males. The oldest animals are generally found at the greatest distance from the coast, sometimes as far out as 5–6 (nautical) miles. [1]

In March and April a general migration takes place, during which zones III and IV are gradually being populated by small females, while the larger females and the males move from zone I to zone II.

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[1] In the winter of 1928–29, during a period of severe frost in January, a conspicuous decrease in the number of larger ♀♀ in zone II and even zone I took place, which shows that migration can sometimes go on until far into winter.

From May until August larger females with eggs can be found both in zone II and zone III. Zone IV contains great numbers of small shrimps, at first consisting of females only; lateron males, too, become numerous.

From August until the second half of October, when the hatching period is over, the larger animals are evenly distributed among zones I, II and III. In zone IV, however, only small animals occur. Details concerning the time of the year when and the regions where hatching of the larvae takes place will be given below.

What can be the meaning of these characteristic seasonal changes in distribution?

In the first place it is conceivable that shrimps (or their eggs or larvae) may not be able to endure exceedingly low temperatures.

Havinga points out that the seasonal migration always takes the animals to the regions of the highest temperature available at the moment. During winter these regions are the North Sea and the deeper creeks of the Dutch shallows, during summer the shallow brackish waters of the Zuyderzee and Scheldt estuaries and a narrow strip along the Dutch coast.

Secondly, seasonal changes in the distribution may be caused, at least in part, by a search for better feeding-grounds. This point is especially stressed by Balss (1930) and Ehrenbaum (1890). It cannot be denied that the brackish regions, where great numbers of shrimps are found during summer, are exceedingly rich in food. In this connection it should be remarked, however, that Havinga only assumes the more restricted and irregular movements to depend on food conditions.

In the third place the typical seasonal distribution could be explained by assuming a combined influence of temperature and salinity. From this point of view the data concerning distribution and migration could be summarized as follows: low temperatures should be accompanied by high salinities, high temperatures by low salinities. This inference, though not directly obvious from the facts described above, is based upon the results of experiments made by Broekhuysen (1936) and Caudri (1937).

Broekhuysen (1936), working with the shore crab, *Carcinides maenas* (L.), attempted to find an explanation for the distribution of this species in the vicinity of Den Helder. This distribution is in many respects similar to that of *Crangon*, the shore crab, like the shrimp, migrating seawards in autumn and back again in spring, but its migrations are less extensive, so that this species does not as a rule reach such high and low salinities. During summer it mainly occurs in water ranging from 10–31 $^0/_{00}$ salinity. The boundary line towards the salt water in the North Sea is rather clearly marked, whereas towards the less saline side the line is not so sharply defined. During winter the area of distribution is much more restricted, consisting only of the salter part of the area inhabited in summer. BROEKHUYSEN tried to find an explanation for these facts by experimentally determining the lowest and highest salinities the species could bear. Since he considered full-grown crabs less suitable for his experiments he decided to study the development of their eggs. Contrary to his expectations he found that no fixed salinity limits existed, as these limits (especially the lower one) depend on temperature. He found that at a temperature of about 16° C a salinity of at least 20 $^0/_{00}$ is necessary for the normal development of the eggs, whereas at a temperature of 8° C the salinity should at least be 26 $^0/_{00}$. Thus, at a higher temperature the lower salinity limit shifted about 6 $^0/_{00}$ in a downward direction. The upper salinity limit for normal development proved to be exceptionally high, lying somewhere between 40 and 50 $^0/_{00}$. No marked influence of temperature upon this limit was found.

These results, although not answering the original purpose of the experiments, as they did not explain the peculiar distribution of the shore crab, give a valuable indication towards solving the question why the area of distribution shows a marked shifting towards more saline water in winter; the more so since some preliminary experiments with full-grown shore crabs pointed to their being in the same way susceptible to a combined influence of temperature and salinity.

A second indication in this direction was given by the outcome of experiments on the influence of temperature and salinity on the death rates of young shrimps made by CAUDRI (1937).

Death rates were determined in seawater of a salinity ranging between 10 and 45 $^0/_{00}$, with 5 $^0/_{00}$ difference between the experiments, one series being tested at 16, another at 4° C. Unforeseen circumstances caused the failure of the "warm" series of experiments. At a temperature of 4° C the minimum death rate was recorded in a salinity of about 34 $^0/_{00}$. This result agrees well with the fact that in severe winters shrimps are mainly living at some distance from the coast, where the salinity does not differ much from the salinity optimum found at this temperature.

Summarizing these indications concerning the combined influence of temperature and salinity on the animals mentioned we can state the following:

1. Concerning *Carcinides:* by a decrease in temperature from ca. 16° C to ca. 8° C the lower salinity limit for normal development of the eggs shifts from 20 to 26 $^0/_{00}$.

2. Concerning *Crangon:* at a temperature of ca. 4° C the optimum salinity is relatively high, ca. 34 $^0/_{00}$.

The object of my own experiments was in the first place to extend the investigations made by Caudri with *Crangon crangon* L. These researches are to be described in the first part of this paper. I further hoped, in case a combined influence of temperature and salinity in *Crangon* could be put beyond doubt not only for lower, but also for higher temperatures, and for younger as well as older stages, to try and analyse the cause of this combined influence. The investigations bearing on this matter are described in part II.

PART I. THE INFLUENCE OF TEMPERATURE AND SALINITY ON THE MORTALITY OF SHRIMPS

Introduction

We saw that the distribution of *Crangon crangon* L. changes with the seasons. In autumn and winter the animals migrate to deeper water farther away from the coast, in spring and summer they return to shallow water. The deeper water in winter is salter and not of such an extremely low temperature as the coastal water. The shallow water in summer is warm, but generally speaking brackish. The change in habitat, then, involves a change in both temperature and salinity, and we first want to settle the relationship between these two factors beyond doubt.

We can ask then:

1. If at a low temperature, of about 4° C, the optimum salinity is a high one (ca. 34 $^0/_{00}$), where lies the optimum salinity which corresponds to the relatively high temperature prevailing in the Dutch Waddenzee during summer? If a combined influence of temperature and salinity as described above can be

shown to exist one would suppose the optimum salinity at such high temperatures to be rather low, at least considerably lower than $34\,{}^{0}/_{00}$.

2. Is the combined influence in question the same for specimens of different ages?

3. What is the influence of temperature upon the salinity limits between which eggs of *Crangon* develop normally?

These questions are dealt with below in the following order:

1. Death rates of shrimps of ca. 2 years old in media of different temperatures and salinities.
2. Death rates of shrimps of ca. 1 year old at a temperature of 22° C in media of different salinities.
3. Death rates of newly hatched larvae in media of different temperatures and salinities.
4. Influence of temperature on the salinity limits between which egg development is normal.

I. Death rates of shrimps of about 2 years old in media of different temperatures and salinities.

In order to determine the influence of different temperatures on the salinity optimum the following experiments were made:

Series 1. Animals kept in seawater of 15, 25, 35 and $45\,{}^{0}/_{00}$ salinity, at a temperature of 22° C.

Series 2. Animals kept in seawater of 15, 25, 35 and $45\,{}^{0}/_{00}$ salinity at a temperature of 16° C.

Series 3. Animals kept in seawater of 15, 25, 35 and $45\,{}^{0}/_{00}$ salinity at a temperature of 12° C.

Series 4. Animals kept in seawater of 15, 25, 35 and $45\,{}^{0}/_{00}$ salinity at a temperature of 3–5° C.

a. METHOD

The length of the specimens considered to be two years old was about 60 mm from front of rostrum to end of tail.

The animals were kept in about 12 l of seawater of a known salinity in glass aquaria of $30 \times 20 \times 20$ cm. There were 4 series of 8 aquaria each, each series being kept at a different temperature. Two out of the 8 aquaria of each series were filled with seawater of $15\,{}^{0}/_{00}$ salinity, 2 with seawater of $25\,{}^{0}/_{00}$ and 2 with 35 and $45\,{}^{0}/_{00}$ seawater respectively. There were thus 32 aquaria in all. The 8 aquaria belonging to one series were all placed into a zinc tank, the remaining space of which was filled with tap water. This water was kept at a constant temperature, which was different for each of the 4 series. The aquaria were somewhat higher than the tank, so that the tap water surrounded them for about $\frac{3}{4}$ of their height. The tanks were covered all around with asbestos plates.

The temperature of the series kept at 22 and 16° C was kept constant by heating the water surrounding the aquaria. To this end 3 carbon filament lamps, each of them in a zinc tube, were placed in the tank between the aquaria in such a way that each aquarium was heated to the same degree. Temperature was kept constant by a thermoregulator and a relay. This was possible, because room temperature was below 16° C. — The temperature of the series kept at 8° C was kept constant by a gentle flow of tap water, which during the experiments had a temperature of about 6° C. — The last series was kept at 4–5° C; the water in the tank was continually cooled by ice.

The seawater within the aquaria was of salinities of 15, 25, 35 and 45 ‰. Much attention was given to the way in which these gradations were obtained. Seawater was brought home from well out at sea in order to have it mixed with as little inland water as possible. It was then made to evaporate at a temperature of ca. 60° C till the salinity had risen to about 70 ‰. From this supply of concentrated seawater the various salinities were obtained by dilution with distilled water. The salinity was then determined titrimetrically with the help of KNUDSEN's tables. Thus, all the solutions differed from each other only in the relative quantities of concentrated seawater and distilled water, and if a change in the seawater would have taken place during evaporation all the solutions would be affected in the same way.

The contents of each aquarium had to be renewed at least once a week. The changing was done in such a way that no temperature or salinity changes were involved. The used seawater was filtered several times over pulverized norit in order to take away the organic matter in solution as much as possible. After that, the salinity was again determined, and if the concentration was found to have changed the original salinity was re-established by addition of the necessary quantity of distilled water. For, as a rule, the salinity during the experiments became slightly higher by evaporation, notwithstanding the fact that all aquaria were covered by glass plates in order to minimize water loss. The solutions thus treated were ready to be used again.

Each aquarium was provided with a thick layer of shell sand, the quantity of which was the same for all aquaria. The shrimps prefer lying hidden just below its surface and the shells presumably prevent the water from becoming somewhat acid by accumulation of carbon dioxide.

Some preliminary experiments showed death rates increasing rapidly when more than 10–12 animals per aquarium were being used. As the aquaria were continually aerated oxygen deficit could not be the cause of this increasing mortality. Moreover, it appeared from an oxygen titration that the presence of 16 animals, kept at a temperature of 22° C, had no noticeable effect on the oxygen content of the aquarium water. Possibly an unfavourable influence was caused by waste products. Anyhow, it appeared necessary to take no more than 8–10 animals per aquarium. This amounted to 16–20 animals (distributed over 2 aquaria) per degree of salinity.

By using 16–20 animals per salinity it was just possible to obtain workable results. By taking a smaller number the influence of temperature and salinity upon death rates may be obscured by the influence of incidental and uncontrollable factors, probably due in part to circumstances under which the animals had been living before they were used for the experiments.

Freshly caught shrimps were never used. Before being used for an experiment the animals were kept for at least a week in the great aquarium basins of the Zoological Station, in which salinity generally amounted to ca. 30 $^{0}/_{00}$. After that, a number of shrimps were kept during one day in aquaria of 25 and 35 $^{0}/_{00}$ salinity, the temperature remaining the same. The next day these animals were transferred into aquaria of 15 and 45 $^{0}/_{00}$ salinity respectively, still at the same temperature.

At the same time the 25 and 35 $^{0}/_{00}$ aquaria were repopulated with fresh animals. On the following 1 or 2 days the temperature was gradually increased or lowered to the desired degree.

Mortality among the animals in each aquarium was checked twice a day. The experiments were carried on until most of the animals had died.

b. Experiments

The results of the first four experiments are represented in abridged form in table 1 (*a* and *b*), 2, 3 and 4, and in the corresponding graphs 1–4.

Series 1. Temperature 22° C

The complete course of events of this series is recorded in table 1*a*. Table 1*b* gives the results in a more convenient arrangement (see also graph 1).

The temperature during the experiment varied between 21.4 and 22.5° C. The salinity extremes are given below:

Salinity in $^{0}/_{00}$	15	25	35	45
maximum	16.2	25.8	37.9	45.9
minimum	15.1	25.1	35.2	44.7

Six animals were eaten by the others during or shortly after moulting; one of them originated from a 15 $^{0}/_{00}$ aquarium, 3 from

TABLE 1*a*

Decrease in the number of animals kept in media of different salinities at a temperature of 22° C

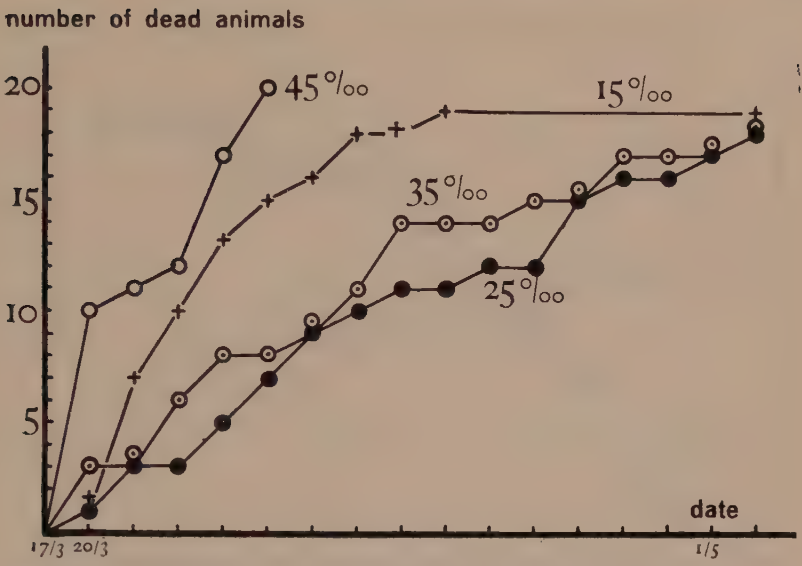
Date	Number of animals per aquarium							
	$15\,^0/_{00}$		$25\,^0/_{00}$		$35\,^0/_{00}$		$45\,^0/_{00}$	
	aquarium 1	aquarium 2	aquarium 1	aquarium 2	aquarium 1	aquarium 2	aquarium 1	aquarium 2
17-3-'38	10	10	10	10	10	10	10	10
20-3-'38	9	10	9	10	9*	8	6	4
23	6	7	8	9*	9	8	6	3
26	4*	6*	8	9	7*	7	6	2
29	1	6	7	8*	6	6	2	1
1-4-'38	1	4	7	6	6	6	0	0
4-4-'38	0	4	7	4	5	6		
7		2	6	4	4	5		
10		2	5	4	3	3		
13		1	5	4	3	3		
16		1	5	3	3	3		
19		1	5	3	2	3		
22		1	3	2	2	3		
25		1	2	2	1	2		
28		1	2	2	1	2		
1-5-'38		1	1	2	1	2		
4-5-'38		1	1	1	0	2		

TABLE 1*b*

Time (expressed in days) elapsing before 5, 10 and 15 animals out of a total number of 20 have died in each salinity. Temp. 22° C.

Salinity	Time in days elapsing before 5 animals have died	Time, etc. 10 animals	Time, etc. 15 animals
$15\,^0/_{00}$	6½	8½	14½
$25\,^0/_{00}$	16½	34½	46
$35\,^0/_{00}$	12	22½	39
$45\,^0/_{00}$	2½	4	11½

a $25\,^0/_{00}$ and 2 from a $35\,^0/_{00}$ aquarium. In table 1*a* these "unnatural death cases" are marked with an asterisk; in the graphs all death cases are recorded without distinguishing between



Graph 1. Death rates of shrimps of ca. 2 years old in media of 15, 25, 35 and 45 °/oo salinity at a temperature of 22° C.

natural and unnatural death. In table 1*b* only those animals which died a "natural" death are accounted for.

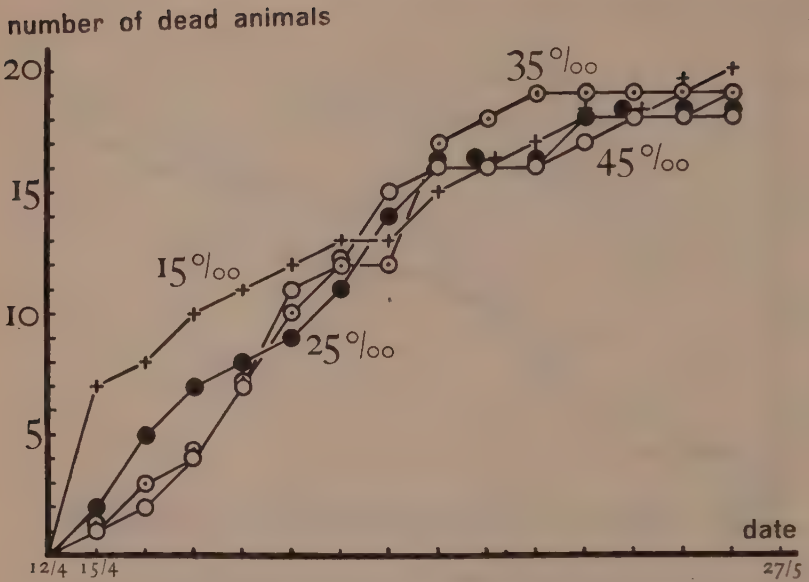
Series 2. Temperature about 17° C

For this series see table 2, which is to be compared with table 1*b*. A table like table 1*a* of the foregoing series, giving the decrease in the number of animals in the media of different salinity, is omitted here as well as furtheron (see also graph 2).

TABLE 2

Time in days elapsing before 5, 10 and 15 animals out of a total number of 20 have died in each salinity. Temp. 17° C

Salinity	Time in days elapsing before 5 animals have died	Time, etc. 10	Time, etc. 15
15 °/oo	3½	11½	25½
25 °/oo	7½	19	23½
35 °/oo	12½	16	21
45 °/oo	12½	16	21



Graph 2. Death rates of shrimps of ca. 2 years old in media of 15, 25, 35 and 45 $^{0}/_{00}$ salinity at a temperature of 17° C.

During the course of the experiment the temperature rose from 15.9 to 19.5° C. Salinity extremes are given below:

Salinity in $^{0}/_{00}$	15	25	35	45
maximum	15.6	26.0	35.1	45.5
minimum	15.0	25.0	34.6	44.5

In this series no cannibalism occurred.

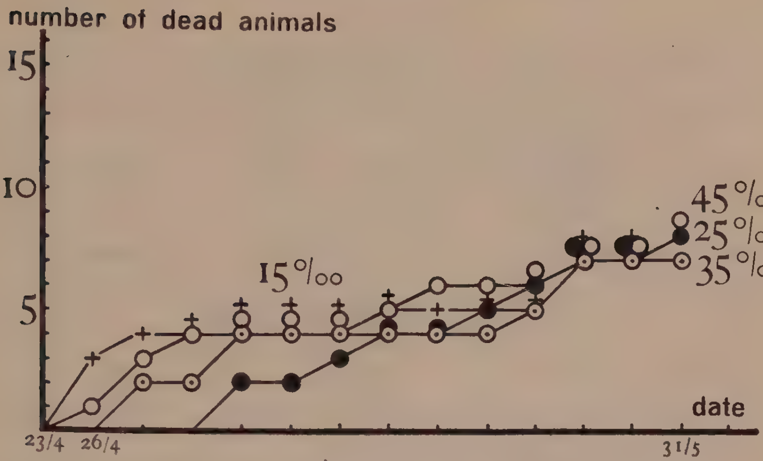
Series 3. Temperature about 12° C

The results of this series can be found in table 3 and the corresponding graph 3.

TABLE 3

Time in days elapsing before 3, 5 and 7 animals out of a total number of 20 have died in each salinity. Temp. 12° C

Salinity	Time in days elapsing before 3 animals have died	Time, etc. 5	Time, etc. 7
15 $^{0}/_{00}$	2½	18½	31
25 $^{0}/_{00}$	20½	31	35½
35 $^{0}/_{00}$	10	29½	31
45 $^{0}/_{00}$	7	23½	35½



Graph 3. Death rates of shrimps of ca. 2 years old in media of 15, 25, 35 and 45 ‰ salinity at a temperature of 12° C.

At the beginning of the experiment the temperature was about 9° C. Owing to a rise in temperature of the tap water used for cooling a gradual rise, to about 13° C, took place. The highest temperature was 14.5° C, but this occurred only during the last few days; the lowest temperature was 9° C. Salinity extremes are given below:

Salinity in ‰	15	25	35	45
maximum	15.9	25.3	35.6	45.4
minimum	15.0	24.9	34.6	44.4

On May the 24th one of the 15 ‰ aquaria suffered from lack of aeration. At this time the aquarium still contained 6 shrimps. As these animals were considerably weakened by oxygen lack the aquarium had to be put out of action. The results of this series are therefore incomplete.

Two animals were eaten by others during or shortly after moulting. One of them belonged to a 45, the other to a 25 ‰ aquarium.

Series 4. Temperature 3–5° C

The results of this series are put together in table 4 and the corresponding graph 4.

TABLE 4

Time in days elapsing before 1, 2, 4 and 8 animals out of a total number of 20 have died in each salinity. Temp. 3–5° C

Salinity	Time in days elapsing before 1 animal has died	Time, etc. 2	Time, etc. 4	Time, etc. 8
15 $^{0}/_{00}$	1½	2½	8	21½
25 $^{0}/_{00}$	11½	30	59½	63½
35 $^{0}/_{00}$	21½	73½		
45 $^{0}/_{00}$	3½	15½	19	37½

The highest temperature was 6.9°, the lowest 2.0° C. The salinity extremes are given below:

Salinity in $^{0}/_{00}$	15	25	35	45
maximum	15.5	25.8	35.4	45.2
minimum	13.4	24.1	34.9	44.4

Four animals were eaten by others during or shortly after moulting; 2 of these belonged to the population of a 25 $^{0}/_{00}$, 2 to that of a 35 $^{0}/_{00}$ solution.

Results of series 1–4

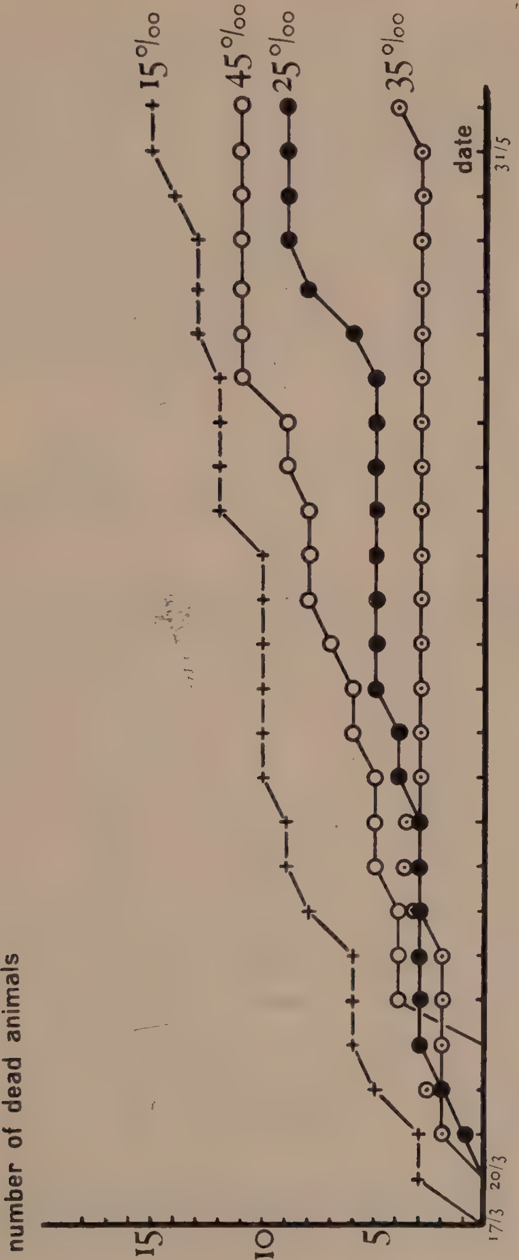
At a temperature of 22° C the salinity optimum seems to be lying somewhere between 25 and 35 $^{0}/_{00}$. Since the death rate in a salinity of 25 $^{0}/_{00}$ was, on the whole, found to be somewhat smaller than in a salinity of 35 $^{0}/_{00}$ the optimum at this temperature may be in the neighbourhood of 29 $^{0}/_{00}$.

Table 1*b* shows that the number of days elapsing before a given number of animals have died is greatest in a salinity of 25 $^{0}/_{00}$.

At a temperature of about 17° C animals kept in various degrees of salinity show no marked difference in mortality; table 2 shows that the number of days elapsing before 15 animals die is about the same for all salinities; anyway, differences are too small to be of any significance.

The same holds for a temperature of about 12° C; it appears from table 3 that the time in which the death of the first 7 animals takes place is about the same for all salinities.

At a temperature of about 4° C death rates in the various



Graph 4. Death rates of shrimps of ca. 2 years old in media of 15, 25, 35 and $45\,^{0}/_{00}$ salinity at a temperature of 3–5° C.

solutions show marked differences. Table 4 shows that the space of time during which a given number of animals die is greatest in 35 $^{0}/_{00}$. In 25 $^{0}/_{00}$, which follows next, it is much smaller, and in 45 and 15 $^{0}/_{00}$ it is smaller still. The optimum therefore lies between 35 and 25 $^{0}/_{00}$, apparently little below 35 $^{0}/_{00}$. This result corresponds with that of CAUDRI, who, experimenting with 5–6 months old shrimps, found a salinity of about 34 $^{0}/_{00}$ to be optimal at a temperature of about 4° C.

The differences in death rates at a temperature of about 22° C (series 1) are rather small. The possibility therefore might exist that they are due to fortuitous causes. In order to make certain about this point the experiments at this temperature were repeated twice over.

Series 5. Temperature about 22° C

The results of this series are given in table and graph 5.

TABLE 5

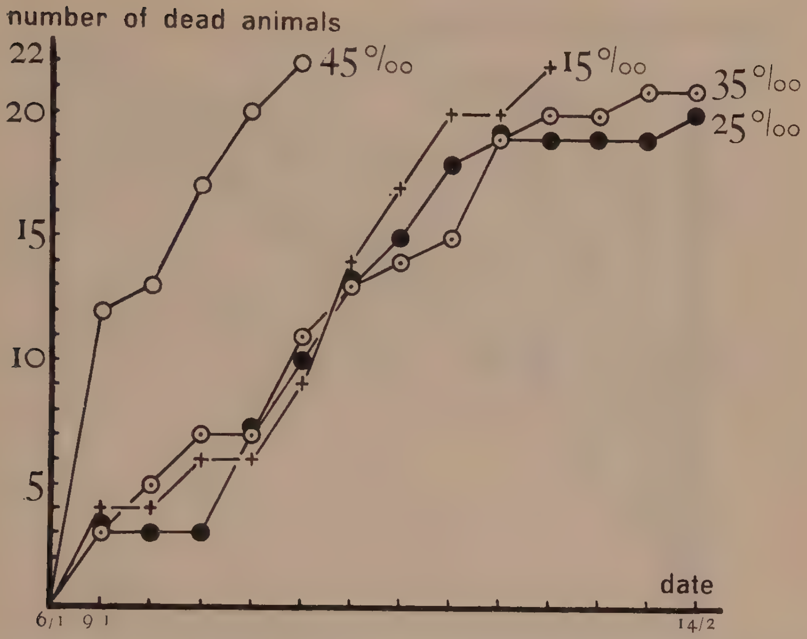
Time in days elapsing before 5, 9, 13 and 17 animals out of a total number of 22 have died in each salinity. Temp. 22° C

Salinity	Time in days elapsing before 5 animals have died	Time, etc. 9	Time, etc. 13	Time, etc. 17
15 $^{0}/_{00}$	9½	15½	18½	22
25 $^{0}/_{00}$	12½	15½	19	27½
35 $^{0}/_{00}$	8½	16½	22½	28
45 $^{0}/_{00}$	2	2½	5½	10

The highest temperature was 22.4°, the lowest 20.0° C. The salinity extremes are given below:

Salinity in $^{0}/_{00}$	15	25	35	45
maximum	15.6	26.0	35.4	45.8
minimum	15.0	25.3	34.8	45.2

Three animals were eaten by others during moulting. Two of them belonged to a salinity of 35 $^{0}/_{00}$, one to a salinity of 25 $^{0}/_{00}$.



Graph 5. Death rates of shrimps of ca. 2 years old in media of 15, 25, 35 and 45 $^0/_{00}$ salinity at a temperature of 22° C.

Series 6. Temperature about 21° C

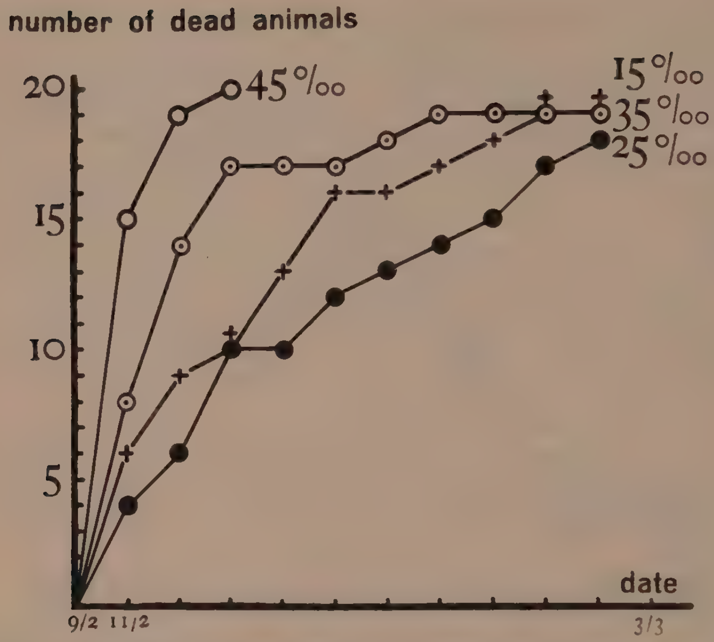
The results of this series are given in table and graph 6.

TABLE 6

Time in days elapsing before 5, 10, 15 and 18 animals out of a total number of 20 have died in each salinity. Temp. 21° C

Salinity	Time in days elapsing before 5 animals have died	Time, etc. 10	Time, etc. 15	Time, etc. 18
15 $^0/_{00}$	1½	7	10½	17½
25 $^0/_{00}$	3½	9½	18	21½
25 $^0/_{00}$	2½	3½	5½	11½
45 $^0/_{00}$	1½	2½	3	4

The highest temperature was 21.5, the lowest 17° C. The latter



Graph 6. Death rates of shrimps of ca. 2 years old in media of 15, 25, 35 and 45 ‰ salinity at a temperature of 21° C.

temperature, caused by the temporary failing of the heating system, only lasted for a short time.

The salinity extremes are given below:

Salinity in ‰	15	25	35	45
maximum	15.6	25.4	35.7	45.4
minimum	14.9	25.1	35.0	45.1

One animal belonging to a salinity of 25 ‰ was eaten by the others during moulting.

Results

On the whole, the results of the second and third 22° C series are similar to that of the first series.

In the second 22° C series (series 5) mortality is about the same in salinities of 15, 25, and 35 ‰. Only during the last stages of the experiment mortality among the animals kept in a salinity of 15 ⁰/₀₀ is greater than in the other two media; hence the salinity optimum at this temperature may be about 28 ⁰/₀₀.

The third 22° C series (series 6) resulted in somewhat greater differences in death rates. The lowest death rate was found in a salinity of 25 ⁰/₀₀. The optimum salinity, however, may be somewhat lower, as mortality (especially during the first stages of the experiment) was lower in 15 than in 35 ⁰/₀₀.

Finally, by experimenting with a narrower salinity range, I attempted to determine the salinity optimum at a temperature of 22° C more precisely. Starting with 20 animals per salinity death rates were recorded in 20, 25, 30 and 35 ⁰/₀₀ degrees of salinity.

Series 7. Temperature 22° C

The results of this series are given in table and graph 7.

TABLE 7.

Time in days elapsing before 5, 10, 15 and 17 animals out of a total number of 20 have died in each salinity. Temp. 22° C

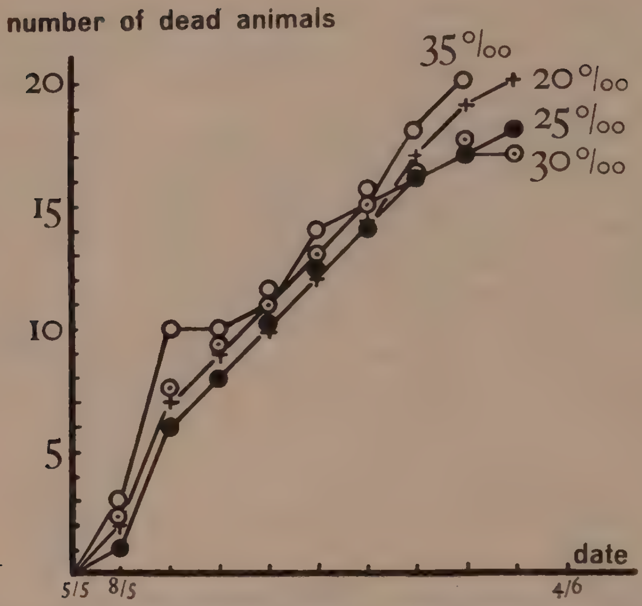
Salinity	Time in days elapsing before 5 animals have died	Time, etc. 10	Time, etc. 15	Time, etc. 17
20 ⁰/₀₀	5	10½	18½	21
25 ⁰/₀₀	4½	10½	18½	22½
30 ⁰/₀₀	5½	9½	17	22½
35 ⁰/₀₀	4	6	16	20

The highest temperature was 23.5°, the lowest 21.8° C. The salinity extremes are given below:

Salinity in ⁰/₀₀	20	25	30	35
maximum	20.2	25.3	31.0	35.2
minimum	20.0	24.9	30.0	35.0

No cannibalism occurred.

As could be expected differences in death rates are only small here. However, mortality among the animals kept in a salinity



Graph 7. Death rates of shrimps of ca. 2 years old in media of 20, 25, 30 and 35 °/$_{00}$ salinity at a temperature of 21° C.

of 35 °/$_{00}$ is somewhat higher than in the other three degrees of salinity. As death rates in these salinities (20, 25 and 30 °/$_{00}$) are about equal this series also leads to the conclusion that a salinity optimum exists near (probably somewhat below) 30 °/$_{00}$.

Summarizing the results of all these experiments we come to the following conclusions:

1. Obvious differences in mortality among animals kept in various degrees of salinity were only found at extreme temperatures, in casu 4° C and 22° C.

2. These differences are the following:
a. At a temperature of 3–5° C the salinity optimum for shrimps of about 2 years old is ca. 33 °/$_{00}$. The highest death rate at this temperature is found in a salinity of 15 °/$_{00}$.
b. At a temperature of about 22° C a rather indistinct optimum is found in the neighbourhood of 25 °/$_{00}$. As two out of

three experiments point to the optimum being higher than $25\,^0/_{00}$ the optimum might be about $28\text{–}29\,^0/_{00}$. The highest death rate at this temperature was found in a salinity of $45\,^0/_{00}$.

3. Under laboratory conditions the duration of life is considerably longer when the animals are kept at a low than when kept at a high temperature. Consequently, death rates in various degrees of salinity at high and low temperatures respectively can only be compared in a relative way. Relatively, the salinity optimum is ca. $28\,^0/_{00}$ at 22° C, ca. $33\,^0/_{00}$ at 4° C. This does not mean, however, that in a salinity of $28\text{–}29\,^0/_{00}$ the average duration of life is longer at 22° than at 4° C. On the contrary, as stated above, the average duration of life is longer at the latter temperature.

II. Death rates of shrimps of ca. one year old (length from rostrum to tail 35–40 mm) at a temperature of 22° C in 15, 25, 35 and $45\,^0/_{00}$ salinity.

This series was undertaken with the intention of determining the salinity optimum at a high temperature for comparatively young animals.

According to Havinga "small" shrimps penetrate earlier and farther into the brackish water. This observation suggests their having a relatively low salinity optimum at a high temperature.

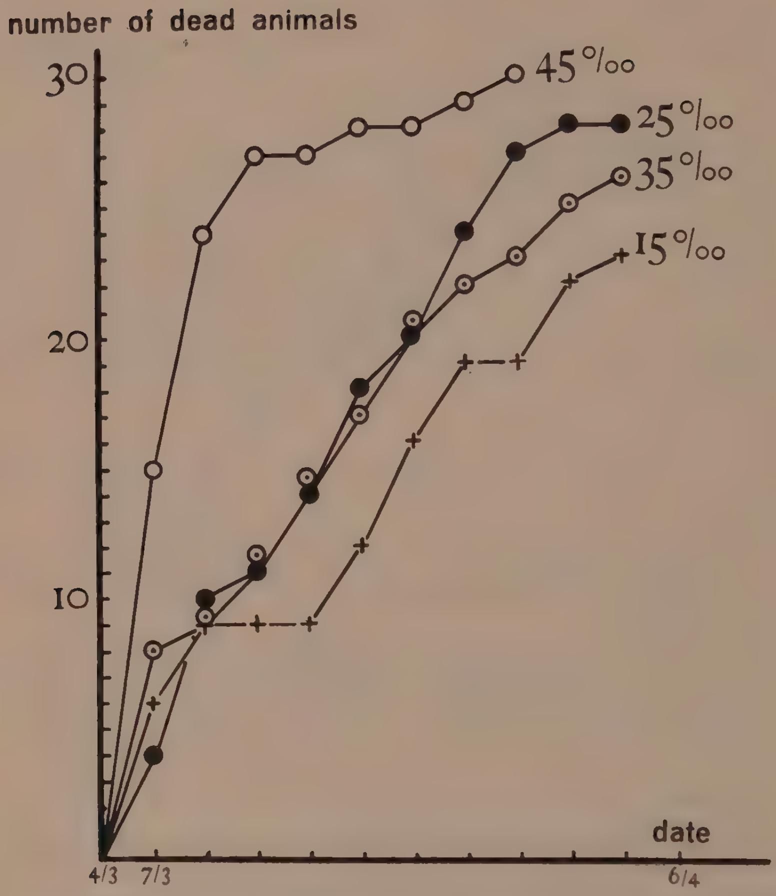
The results of this series are recorded in table and graph 8.

TABLE 8

Time in days elapsing before 6, 11, 16 and 21 animals out of a total number of 30 have died in each salinity. Temp. 22° C

Salinity	Time in days elapsing before 6 animals have died	Time, etc. 11	Time, etc. 16	Time, etc. 21
$15\,^0/_{00}$	4	16½	20	30½
$25\,^0/_{00}$	4½	12	16	22
$35\,^0/_{00}$	3	10½	15½	22
$45\,^0/_{00}$	2½	4	4½	7

Highest temperature 21.8° C, lowest temperature 21° C. Due to a temporary failing of the heating system the temperature



Graph 8. Death rates of shrimps of ca. 1 year old in media of 15, 25, 35 and 45 °/₀₀ salinity at a temperature of 22° C.

one night fell to 13° C, but for a few hours only. The salinity extremes are given below:

Salinity in °/₀₀	15	25	35	45
maximum	15·3	25·9	35·3	45·4
minimum	15.0	25·3	34·9	44·9

Eight animals were eaten by others during or shortly after moulting. Two of these belonged to the population of a 15 °/₀₀, two to that of a 25 ‰, one to that of a 35 ‰ and three to that of a 45 ‰ solution.

Apparently, for young shrimps the salinity optimum at a temperature of 22° C lies in the vicinity of 15 ‰. This is indeed a considerably lower salinity optimum than was found for the older animals. That a salinity of 15 ‰ was really the most favourable also appeared from the behaviour of the animals in this salinity; on the whole they were more lively and consumed more food than in the higher degrees of salinity.

III. Death rates of newly hatched larvae in media of different temperature and salinity.

a. METHOD

The larvae used for these experiments mostly came from females of about two years old, which were kept for the purpose of the experiments recorded under I. During the course of the latter experiments it often occurred that large numbers of larvae made their appearance in one of the aquaria in which death rates were being checked. These larvae, all of which hatched at practically the same time in a medium of known temperature and salinity, were too valuable a material not to be used for further study. Unless stated otherwise, they were used 1–2 days after hatching.

The larvae were distributed over a number of small glass jars. These jars, containing ca. 100 cc of seawater of known salinity, were set out in 3 or more series. Each of these consisted of 3–4 different salinities, and was kept at a constant temperature ranging between 4 and 22° C. The transfer of the larvae in media of different salinity was always carried out suddenly, without intermediate steps. Temperature changes were applied gradually, although over a very short space of time, about half an hour as a rule.

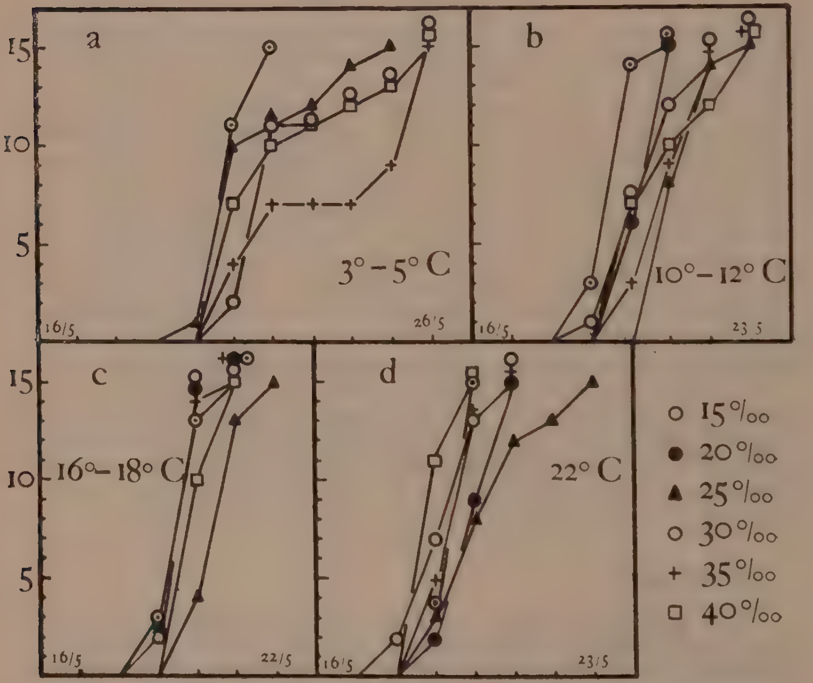
The larvae were fed with plankton. Generally, they lived only for about 12 days. Notwithstanding this very short duration of life death rates proved to be different for animals kept under different temperature and salinity conditions. Since it proved to be impossible to discern death with the naked eye the larvae were pipetted on an object slide and examined microscopically. Ceasing of the rectal respiration served as a criterion for death.

b. EXPERIMENTS

1. The first larvae used for experiments had hatched in seawater of 30 ‰ salinity and at a temperature of about 22° C. They were used for 4 series of experiments, each of which was composed of salinity degrees of 15, 20, 25, 30, 35 and 40 ‰. The four series were kept at temperatures of 22, 16–18, 10–12 and 3–5° C respectively. The number of larvae per salinity was 15. One series therefore contained 105 and the four series together 420 specimens.

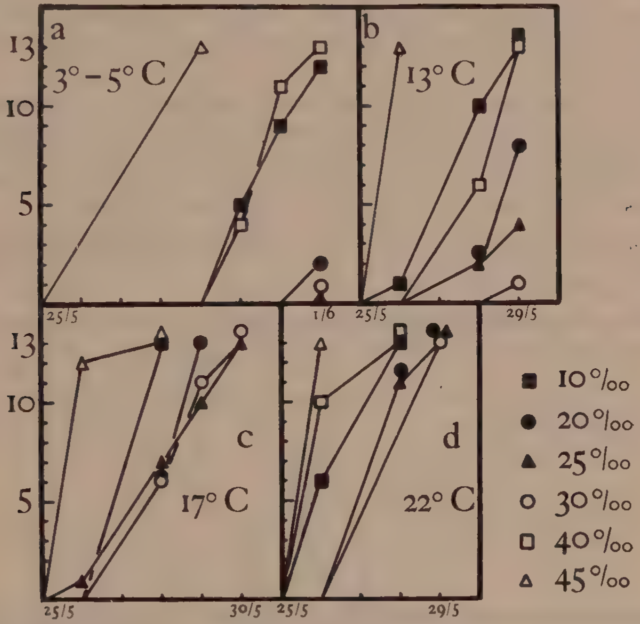
The salinity optima found for the various temperatures are given below. They should be consulted together with the graphs (9*a*, 9*b*, 9*c* and 9*d*).

Temperature	Optimum
3–5° C	ca. 35 $^0/_{00}$
10–12° C	ca. 32.5 $^0/_{00}$, which represents the average between 25, 30, 35 and 40 $^0/_{00}$, death rates being the same in each of these salinities
16–18° C	ca. 25 $^0/_{00}$
22° C	somewhat below 25 $^0/_{00}$, since the death rate during the first days of the experiment was lower in 20 than in 30 $^0/_{00}$



Graph 9. Death rates of shrimp larvae in media of 15, 20, 25, 30, 35 and 40 $^0/_{00}$ salinity at temperatures of 3–5, 10–12, 16–18 and 22° C. In all graphs no. 9 – no. 18 the number of dead animals is plotted vertically, the date horizontally.

The data point to a shifting of the salinity optimum towards the fresher side of the salinity range when temperature is increased. From the graphs this becomes especially clear by comparing the position of the 25 $^{0}/_{00}$ death curve with respect to the position of the other curves. With increasing temperature the position of the 25 $^{0}/_{00}$ curve gradually shifts towards the right side of the graph (which means that it becomes more and more favourable), while the 30, 35 and 40 $^{0}/_{00}$ curves are successively passed.



Graph 10. Death rates of shrimp larvae in media of 10, 20, 25, 30, 40 and 45 $^{0}/_{00}$ salinity at temperatures of 3–5, 13, 17 and 22° C.

2. The larvae used for this experiment had hatched in a salinity of 25 $^{0}/_{00}$ and at a temperature of 13° C. The experiment consisted of 4 series, each series containing salinities of 10, 20, 25, 30, 40 and 45 $^{0}/_{00}$. They were kept at temperatures of 22, 17, 13 and 3–5° C. The number of larvae per salinity was 13, their total number therefore 312.

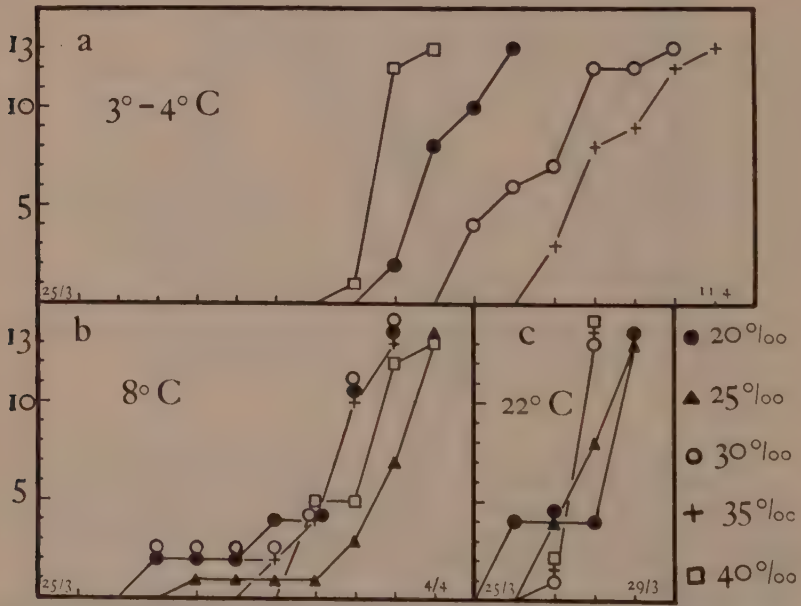
The salinity optima for the various temperatures follow below. Compare graphs 10, *a–d*.

Temperature	Optimum
3–5° C	between 25 and 30 $^{0}/_{00}$
13° C	somewhat below 30 $^{0}/_{00}$, 20 being more favourable than 40 $^{0}/_{00}$
17° C	somewhat above 25 $^{0}/_{00}$, 20 being somewhat less favourable than 25 and 30 $^{0}/_{00}$
22° C	about 25 $^{0}/_{00}$ (similar course of 20, 25 and 30 $^{0}/_{00}$ curves)

In this case the shifting of the salinity optimum with increasing temperature is not very distinct, owing to the deviating outcome of the 3–5° C series; this deviation is discussed furtheron.

3. The larvae used for this experiment had hatched in a salinity of 30 $^{0}/_{00}$ at a temperature of 16° C. The experiment consisted of 3 series, each series containing salinities of 20, 25, 30, 35 and 40 $^{0}/_{00}$. The 3 series were kept at temperatures of 3–4°, 8° and 22° C respectively. The number of larvae per salinity was 13, their total number therefore 195.

The salinity optima for the various temperatures follow below. See also graphs 11, *a–c*.

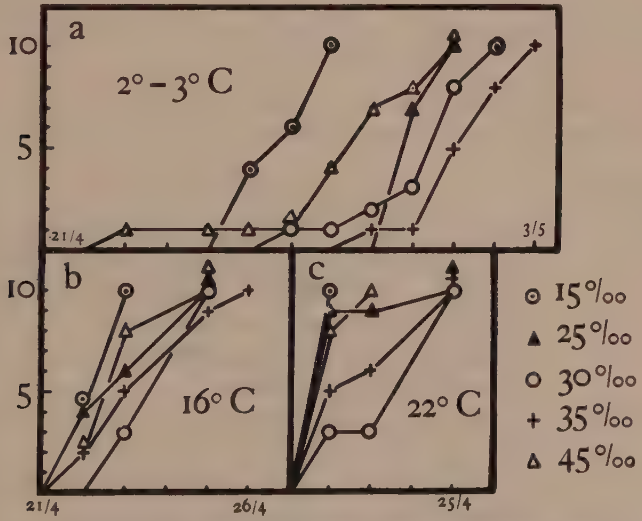


Graph 11. Death rates of shrimp larvae in media of 20, 25, 30, 35 and 40 $^{0}/_{00}$ salinity, at temperatures of 3–4, 8 and 22° C.

Temperature	Optimum
3–4° C	35 $^0/_{00}$ The larvae which were kept in a salinity of 25 $^0/_{00}$ were lost by accident. It is very improbable, however, that 25 $^0/_{00}$ would have been more favourable than 35 $^0/_{00}$, as 30 $^0/_{00}$ proved to be less favourable than 35 $^0/_{00}$
8° C	25 $^0/_{00}$
22° C	between 20 and 25 $^0/_{00}$, probably nearest to 20 $^0/_{00}$

This series of experiments again showed a marked shifting of the salinity optimum towards fresher water with increasing temperature. A comparison of the mutual position of the 20 and 30 $^0/_{00}$ curves at different temperatures can serve to make this clear: at a temperature of 22° C a salinity of 20 $^0/_{00}$ is more favourable than a salinity of 30 $^0/_{00}$; at 8° C 20 and 30 $^0/_{00}$ are equally favourable, at 3–4° C 30 $^0/_{00}$ is more favourable than 20 $^0/_{00}$.

4. The larvae used for this experiment had hatched in a salinity of 45 $^0/_{00}$ at a temperature of 16° C. The experiment consisted of 3 series,



Graph 12. Death rates of shrimp larvae in media of 15, 25, 30, 35 and 45 $^0/_{00}$ salinity, at temperatures of 2–3, 16 and 22° C.

each series containing salinities of 15, 25, 30, 35 and 45 $^0/_{00}$. They were kept at temperatures of 2–3, 16 and 22°C. The number of larvae per salinity was 10, their total number 150.

The salinity optima for the various temperatures follow below. See also graphs 12, *a–c*.

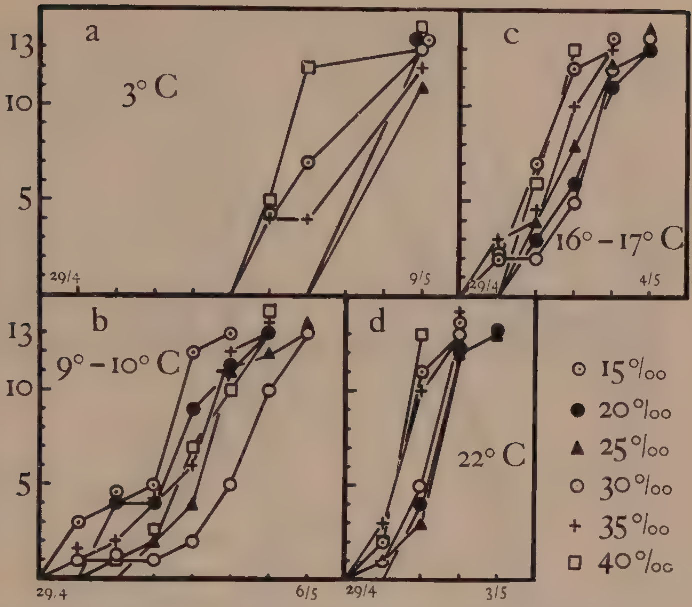
Temperature	Optimum
2–3° C	ca. 35 $^0/_{00}$
16° C	ca. 33 $^0/_{00}$ (35 $^0/_{00}$ is the most favourable salinity, immediately followed by 30 $^0/_{00}$)
22° C	31 or 32 $^0/_{00}$ (30 $^0/_{00}$ is the most favourable salinity, 35 $^0/_{00}$ is more favourable than 25 $^0/_{00}$)

Here, too, shifting of the salinity optimum can be observed, although differences are only slight. The fact that all salinity optima are relatively high may be due to the extremely high salinity (45 $^0/_{00}$) in which the larvae had hatched. In the lower degrees of salinity these larvae, while still living, showed considerable swelling.

5. The larvae used for this experiment had hatched in a salinity of 30 $^0/_{00}$, at a temperature of 15° C. The experiment consisted of 4 series, each series containing salinities of 15, 20, 25, 30, 35 and 40 $^0/_{00}$. The series were kept at temperatures of 3, 9–10, 16–17 and 22°C. The number of larvae per salinity was 13, the total number 312.

The salinity optima for the various temperatures are given below. Compare also graph 13, *a–d*.

Temperature	Optimum
2–3° C	No clearly marked optimum. In salinities of 15 and 20 $^0/_{00}$ swelling of the larvae occurred. A salinity of 40 $^0/_{00}$ was distinctly unfavourable. The course of mortality in the remaining degrees can hardly be followed, since observations on the 7th and 8th of March are lacking.
9–10° C	ca. 28 $^0/_{00}$ (30 $^0/_{00}$ somewhat more favourable than 25 $^0/_{00}$)
16–17° C	ca. 25 $^0/_{00}$ (20 $^0/_{00}$, 25 $^0/_{00}$ and 30 $^0/_{00}$ about equally favourable)
22° C	ca. 23 $^0/_{00}$ (25 $^0/_{00}$ somewhat more favourable than 20 $^0/_{00}$).



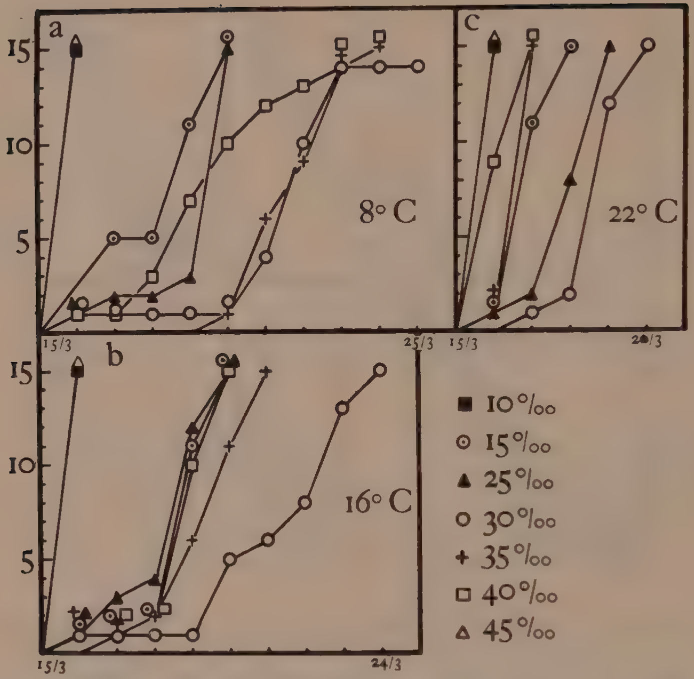
Graph 13. Death rates of shrimp larvae in media of 15, 20, 25, 30, 35 and 40 $^0/_{00}$ salinity at temperatures of 3, 9–10, 16–17, and 22° C.

Shifting of the salinity optimum is clearly illustrated by the mutual position of the 20 and 30 $^0/_{00}$ curves at different temperatures; at a temperature of 9–10° C 30 $^0/_{00}$ is more favourable than 20 $^0/_{00}$, at 16–17° C the two curves show similar courses, at 22° C 20 $^0/_{00}$ is more favourable than 30 $^0/_{00}$.

6. The larvae used for this experiment had hatched in a salinity of 30 $^0/_{00}$ at a temperature of 16° C. The experiment consisted of 3 series, each series containing salinities of 10, 15, 25, 30, 35, 40 and 45 $^0/_{00}$. The series were kept at temperatures of 8, 16 and 22° C. The number of larvae per salinity was 15, their total number 315.

The salinity optima for the various temperatures are given below. See also graph 14, *a–c*.

Temperature	Optimum
8° C	33 $^0/_{00}$ (30 $^0/_{00}$ and 35 $^0/_{00}$ are equally favourable, 40 $^0/_{00}$ is also comparatively favourable)
16° C	ca. 30 $^0/_{00}$ (perhaps somewhat over 30 $^0/_{00}$, as 35 $^0/_{00}$ is slightly more favourable than 25 $^0/_{00}$)
22° C	ca. 28 $^0/_{00}$ (30 $^0/_{00}$ somewhat more favourable than 25 $^0/_{00}$)

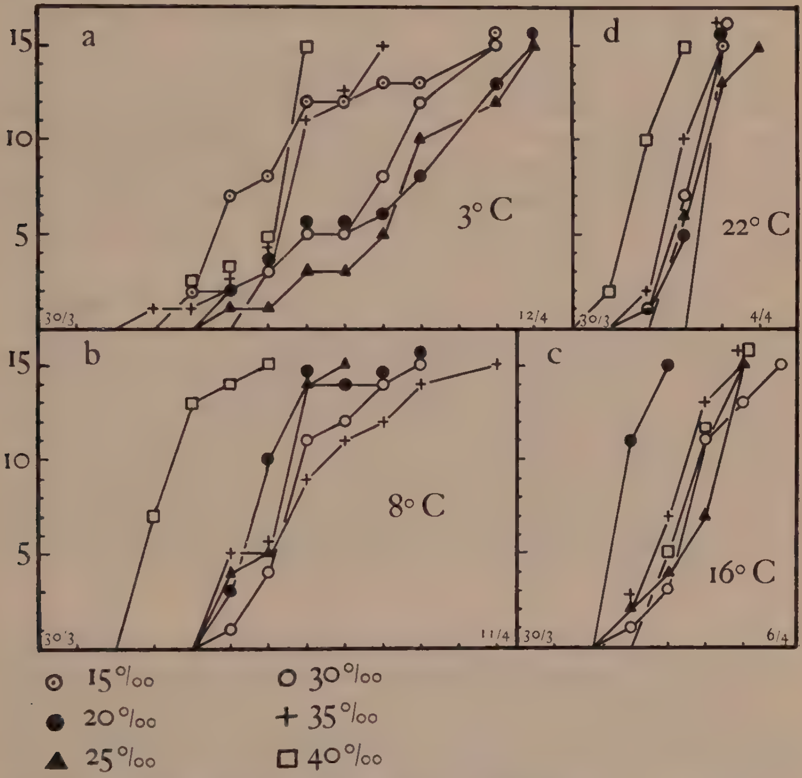


Graph 14. Death rates of shrimp larvae in media of 10, 15, 25, 30, 35, 40 and 45 $^0/_{00}$ salinity at temperatures of 8, 16 and 22° C.

In a salinity of 10 $^0/_{00}$, irrespective whether temperature is low or high, all larvae die within 30 seconds. When transferred into this salinity they always react in a peculiar way, swimming furiously about for 10–20 seconds. It seems clear that this is a reaction to the extremely low salinity. No such reaction was ever seen when larvae were transferred into media of very high salinity, for instance 45 $^0/_{00}$. Neither was a similar reaction ever observed with full-grown shrimps even when transferred into tapwater, nor in a salinity as high as 45 to 50 $^0/_{00}$. In a salinity of 45 $^0/_{00}$, too, the larvae were dead in a short time, 2–3 hours.

Shifting of the salinity optimum with increasing temperature can be followed by comparing the course of the 25, 30 and 35 $^0/_{00}$ curves in relation to each other at different temperatures.

7. The larvae used for this experiment had hatched in a salinity of $25\,^0/_{00}$ at a temperature of 22° C. The experiment consisted of 4 series, each series containing salinities of 15, 20, 25, 30, 35 and $40\,^0/_{00}$. The series were kept at temperatures of 3, 8, 16 and 22° C. The number of larvae per salinity was 15, their total number 330.



Graph 15. Death rates of shrimp larvae in media of 15, 20, 25, 30, 35 and $40\,^0/_{00}$ salinity at temperatures of 3, 8, 16 and 22° C.

The salinity optima for the various temperatures are given below. See also graph 15, *a–d*.

Temperature	Optimum
3° C	somewhat below $25\,^0/_{00}$ ($20\,^0/_{00}$ is more favourable than $30\,^0/_{00}$, $25\,^0/_{00}$ is the most favourable salinity)

8° C	somewhat below 35 $^0/_{00}$ (30 $^0/_{00}$ more favourable than 40 $^0/_{00}$, 35 $^0/_{00}$ the most favourable salinity)
16° C	somewhat below 30 $^0/_{00}$ (25 $^0/_{00}$ more favourable than 35 $^0/_{00}$, 30 $^0/_{00}$ the most favourable salinity)
22° C	somewhat below 25 $^0/_{00}$ (20 $^0/_{00}$ more favourable than 30 $^0/_{00}$, 25 $^0/_{00}$ the most favourable salinity)

Apart from the outcome of the 3° C series the salinity optimum can again be observed to shift in a downward direction with increasing temperature. This becomes particularly clear by comparing the position of the 25 and 35 $^0/_{00}$ curves in relation to each other at different temperatures. The deviating results obtained at a temperature of 3° C will be discussed on p. 36.

8. The larvae which were used for this experiment were taken from a large aquarium (salinity about 29 $^0/_{00}$, temperature about 7° C), containing about 100 full-grown shrimps. The greater part of these consisted of egg-bearing females. Consequently, the material for this experiment was not so uniform as in the other cases. Probably larvae of different age and origin were used, although they showed no apparent differences in size. They were older than the larvae used in the previous experiments, about 1–2 weeks instead of 1–2 days.

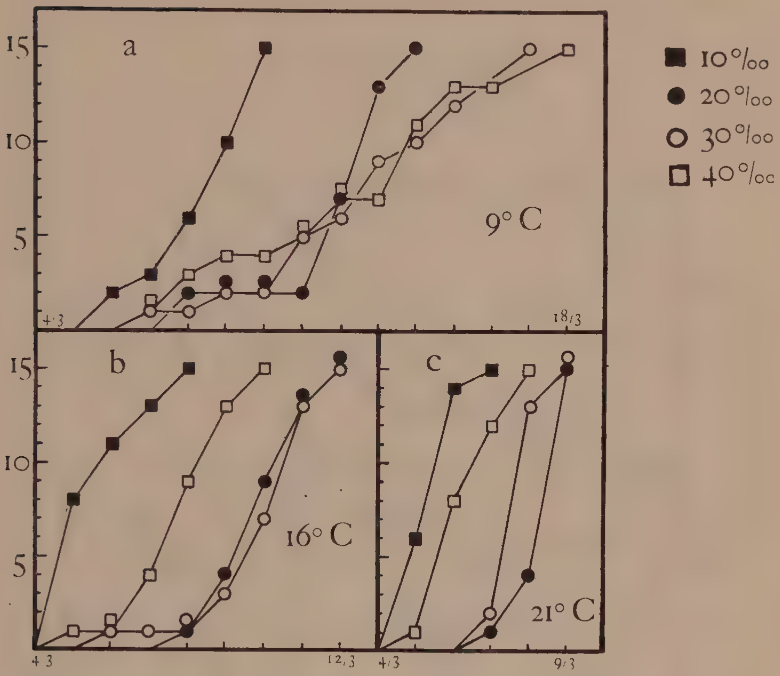
The experiment consisted of 3 series, each series containing salinities of 10, 20, 30 and 40 $^0/_{00}$. The series were kept at temperatures of 9, 16 and 22° C respectively. The number of larvae per salinity was 15, their total number therefore 180.

In connection with the result of experiment 6 it is of interest to note that the larvae used for experiment 8 proved to be able to live for some days in a salinity of only 10 $^0/_{00}$. The different results obtained with both sets of larvae can possibly be explained by the fact that for experiment 8 larvae of 1–2 weeks were used, whereas in the case of experiment 6 the larvae had newly hatched.

The salinity optima for the various temperatures are given below. See also graph 16, *a–c*.

Temperature	Optimum
9° C	ca. 35 $^0/_{00}$ (30 and 40 $^0/_{00}$ equally favourable)
16° C	ca. 26 $^0/_{00}$ (30 $^0/_{00}$ more favourable than 20 $^0/_{00}$)
22° C	ca. 23 $^0/_{00}$ (20 $^0/_{00}$ more favourable than 30 $^0/_{00}$)

Shifting of the salinity optimum can be easily followed.



Graph 16. Death rates of shrimp larvae in media of 10, 20, 30 and 40 $^0/_{00}$ salinity at temperatures of 9, 16 and 22° C.

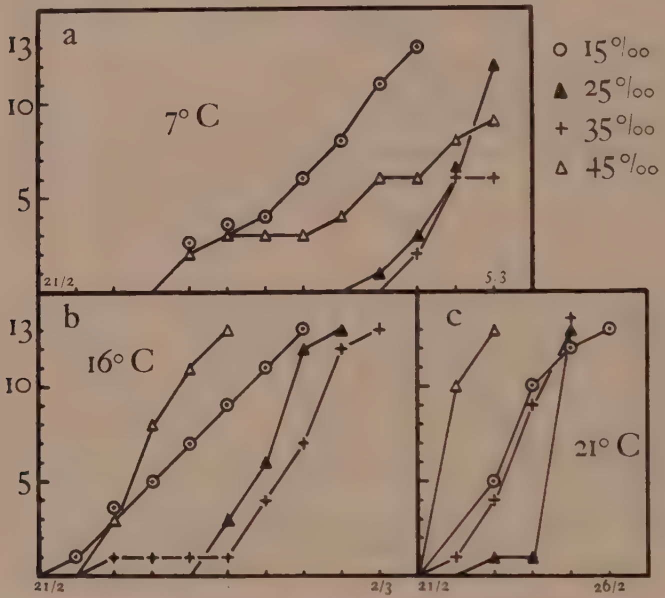
9. The larvae used for this experiment were taken from the same aquarium as the larvae used for experiment 8. Their age probably varied between one and two weeks.

The experiment consisted of 3 series, each series containing salinities of 15, 25, 35 and 45 $^0/_{00}$. The series were kept at temperatures of 7, 16 and 21° C respectively. The number of larvae per salinity was 13, their total number 156.

In connection with the outcome of the experiments 2 and 6 it is of interest to note that the larvae could stand a salinity of 45 $^0/_{00}$ pretty well, especially at a temperature of 7° C. In this case, too, the fact that the larvae were somewhat older than those used for the experiments 2 and 6 may be responsible for their different conduct.

The salinity optima for the various temperatures are given below. See also graph 17, *a–c*.

Temperature	Optimum
7° C	somewhat above 35 $^{0}/_{00}$
16° C	between 25 and 35 $^{0}/_{00}$
21° C	ca. 25 $^{0}/_{00}$

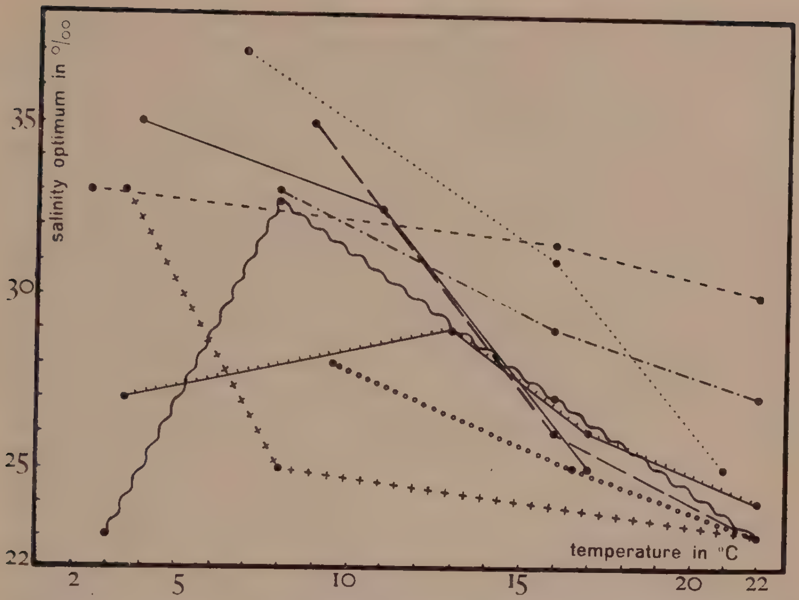


Graph 17. Death rates of shrimp larvae in media of 15, 25, 35 and 45 $^{0}/_{00}$ salinity at temperatures of 7, 16 and 21° C.

The experiment had to be broken off before all larvae kept in the 7° C series had died. At the end of the experiment the number of survivors was greatest in salinities of 35 and 45 $^{0}/_{00}$.

Summary (see graph 18)

On the whole, 9 experiments, each consisting of a great number of temperature-salinity combinations, were carried out. In 7 of these experiments the salinity optimum was found to shift in a downward direction with increasing temperature. The results of two experiments in so far formed an exception that at a low temperature (3–5° C) the optimum proved to be relatively low (27 and 23 $^{0}/_{00}$ respectively). Apart



Graph 18. Salinity optima at various temperatures for newly hatched shrimp larvae. Hatching of the larvae took place in media of the following temperatures and salinities:

———————	30 $^0/_{00}$	22° C.	(exp. 1)
┴┴┴┴┴┴┴┴┴	25 $^0/_{00}$	13° C.	(exp. 2)
+ + + + + + +	30 $^0/_{00}$	16° C.	(exp. 3)
- - - - - - - - -	45 $^0/_{00}$	16° C.	(exp. 4)
• • • • • • • • • • •	30 $^0/_{00}$	15° C.	(exp. 5)
-·-·-·-·-	30 $^0/_{00}$	16° C.	(exp. 6)
〰〰〰	25 $^0/_{00}$	22° C.	(exp. 7)
—— —— ——	29 $^0/_{00}$	7° C.	(exp. 8)
·················	29 $^0/_{00}$	7° C.	(exp. 9)

from these two experiments the salinity optima at a temperature of 3–7° C ranged between 33 and 37 $^0/_{00}$, whereas at 21–22° C they varied between 23 and 27 (in one case 30) $^0/_{00}$. At intermediate temperatures the position of the optima is rather irregular. At ca. 16° C the optima ranged between 24 and 33 $^0/_{00}$, at 8° C between 25 and 35 $^0/_{00}$.

It appears highly probable that the temperature and salinity in which the development and the hatching of the larvae took place have considerable influence on the position of the optima. First of all, the larvae which were used for experiment 4 hatched in a salinity of 45 $^0/_{00}$, which may be called extremely high. All optima, especially those for high temperatures, in this case proved to be relatively high; at 22°C the optimum was 30 $^0/_{00}$, whereas in all other cases it lay below 27 $^0/_{00}$. Secondly, the larvae used for experiments 7 and 2 hatched in the comparatively low salinity of 25 $^0/_{00}$, at rather high temperatures, 22 and 13° C respectively. In these cases all salinity optima, especially at low temperatures, proved to be exceptionally low.

In the foregoing pages we met with some few cases in which the optimum salinity for a low temperature was low instead of high. In experiment 2 the optimum for 3–5° C was lying between 25 and 30 $^0/_{00}$, in experiment 7 the optimum for 3° C was even below 25 $^0/_{00}$. The explanation may be that the temperature changes for these larvae were too great. In experiment 2 the change was from 13 to 3–5° C, in experiment 7 from 22 to 3° C. Consequently, in these cases the larvae were subjected not only to changes in salinity, but also to a change in temperature of in one case 10, in the other 19° C. This may be more than the larvae can stand, and it is probably the reason why they soon come to an end especially in the high salinities, where the salinity change is greater than in the low salinities.

IV. Influence of temperature on the salinity limits for the development of the eggs.

As was stated in the introduction experiments by Broekhuysen (1936) indicated that the salinity limits for the development of *Carcinides* eggs (especially the lower limit) shift in a downward direction with increasing temperature. Similar experiments by Amemiya (1928) with the eggs of *Ostrea gigas* led to conclusions which are more or less opposite to those obtained by Broekhuysen: "thus it is certain that at a low temperature the range of salinity which is available for the development of the oyster is wider than at a high temperature: the range extends more towards higher as well as lower grades of salinity. Especially in the lower part of the range the development becomes rather more favourable."

According to Amemiya the salinity optimum for the development of *Ostrea* eggs is 20–26 $^0/_{00}$ at 23–26° C and 17–26 $^0/_{00}$ at

16° C. In connection with these data AMEMIYA mentions the fact that in the northern part of Japan *Ostrea gigas* lives in water of a very low salinity (in lagoons, estuaries and near river mouths). According to AMEMIYA the low temperature of that region may possibly have a favourable influence on the development of the oyster in water of such a low salinity.

At first sight the behaviour of *Ostrea* seems to be just the opposite to that of *Carcinides*. BROEKHUYSEN points out, however, that possibly both *Carcinides* and *Ostrea* eggs have their widest salinity range at 16° C, and that the range would become narrower both at temperatures higher and lower than 16° C. Thus, the discrepancy between the results of AMEMIYA and those of BROEKHUYSEN would solely be caused by the fact that BROEKHUYSEN worked with temperatures below, AMEMIYA with temperatures above 16° C.

My experiments with full-grown shrimps and shrimp larvae do not support this suggestion. In these animals the available salinity range steadily shifted downwards with temperature increasing from little above 0 to above 20° C and no indication was found of an "optimum temperature", at which the salinity range would have its greatest extent.

For a detailed description of the embryology of *Crangon* I refer to EHRENBAUM (1890). The eggs are attached to the abdomen of the parent animal until the time of hatching. Cleavage takes place soon after spawning. After the conclusion of this process, which leads to the formation of the blastoderm, a yolk-free part begins to become visible. Soon afterwards gastrulation takes place, followed by the appearance of optic discs and of the thoracic-abdominal plate. Thereupon, three pairs of limbs make their appearance. This Nauplius stage is followed by the appearance of another four pairs of limbs. At the same time a single spot of pigment (the Nauplius eye) becomes visible between the optic discs. Soon after the appearance of the Nauplius eye the first indications of the compound eyes become visible, followed by the appearance of numerous pigment spots on head, body and limbs. Meanwhile, the yolk decreases steadily in size, the heart can be seen pulsating, and rhythmical movements of the rectum suggest the beginning of larval respiration. During the last few days before hatching the limbs show convulsive movements. Finally, having attained the zoea stage, the larva hatches. It now possesses 2 pairs of antennae, 1 pair of mandibulae, 2 pairs of maxillae and 3 pairs of maxillipeds, whereas the abdomen is still without limbs.

a. METHOD

The development of shrimp eggs was examined in 8 salinities, ranging between 10 and 45 $^0/_{00}$, with differences of 5 $^0/_{00}$ between the successive grades. This series of salinities was combined with 2 temperatures, viz. 8 and 16° C. The 16° C experiment was carried out twice.

At the beginning of each experiment I selected a great number of females, all bearing eggs in an early stage of development. Since the number of females whose eggs showed as yet no yolk-free part proved to be very small I partly had to take animals with eggs in which the embryo was already visible. I took care, however, not to take them as soon as they showed the beginning of pigmentation. The egg-bearing females were gradually, by steps of 5 $^0/_{00}$ and an interval of one day, transferred into the various media. In this way it took the animals 4–5 days to reach their final salinity. In the meantime, egg development often proceeded to a stage in which formation of the Nauplius eye, or even of the compound eyes, had already begun.

In each salinity 4 egg-bearing females were kept until the eggs hatched. The basins in which they lived contained a shallow layer of water; the bottom was covered with shell sand. During the experiment the water generally remained clear; in some cases it had to be changed once, in other cases not at all. During the course of the experiments, especially in the 16° C series, the concentration rose steadily. The variations in salinity during the course of an experiment sometimes amounted to 2–3 $^0/_{00}$.

Every other day the eggs were inspected and their stage of development recorded by drawing or description. For this purpose a small number of eggs were taken from the parent animal by means of a little spatula.

The eggs were examined microscopically under a low power. The animals of each set of 4 females had been marked individually by amputation of a part of one or both antennae.

The degree of development was judged by the following criteria, and the observations are schematically reproduced as given below:

1. Eggs containing no yolk-free space: ○
2. Embryo just becoming visible: ◔
3. Nauplius eye just becoming visible: ◔
4. Compound eye just becoming visible: ◐
5. Pigmentation on head and limbs: ◕
6. Beginning of heart pulsations: ◕
7. Convulsive movements of limbs (about to hatch): ◕
8. Hatched: ●

Abnormal development is indicated by shading; ◔ for instance means that the nauplius eye has just become visible, the embryos, however, distinguishing themselves in some way or other from normal ones. When normal as well as abnormal development occurred, this is indicated in the following way: ◔

I further used the following symbols:

+ = death of a parent animal during the course of an experiment.
× = parent animal has lost all eggs.
◕ = parent animal has lost part of its eggs.

b. EXPERIMENTS

Series 1. Temperature ca. 9° C. See fig. 2 for schematic reproduction of the results.

Salinities at the beginning of the experiment amounted to 10.3, 15.6, 20.3, 25.3, 29.5, 35.3, 40.0 and 45.4 $^{0}/_{00}$. At the end of the experiment those in the 25 $^{0}/_{00}$ and 45 $^{0}/_{00}$ basins proved to be 26.2 and 46.3 $^{0}/_{00}$ respectively. It may therefore be assumed that during the experiment all salinities increased by about 1 $^{0}/_{00}$.

In the course of the experiment a number of females died; 3 of these belonged to a salinity of 10 $^{0}/_{00}$, 3 to 15 $^{0}/_{00}$, 1 to 25 $^{0}/_{00}$, 3 to 30 $^{0}/_{00}$, 1 to 35 $^{0}/_{00}$, 1 to 40 $^{0}/_{00}$ and 3 to 45 $^{0}/_{00}$.

10 $^{0}/_{00}$. At the time the first inspection took place the Nauplius eye already began to show. Development was normal up to the stage where pulsation of the heart sets in. From this stage on the yolk rest did not decrease in size. Moreover, it consisted of abnormal looking cells of a granular structure. At a later stage, although faint movements of the limbs were visible, still

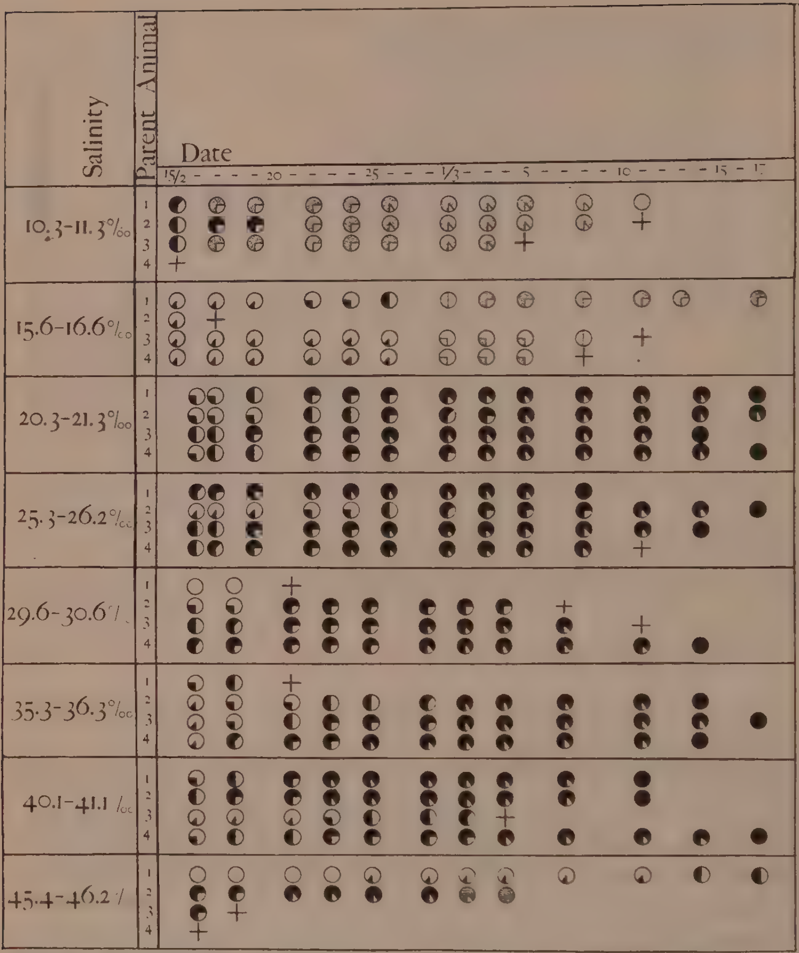


Fig. 2. Development of shrimp eggs in media of ca. 10, 15, 20, 25, 30, 35, 40 and 45 $^{0}/_{00}$ salinity at a temperature of ca. 9° C.

more abnormalities could be observed: the eye pigment grew into irregular radiate streaks and the head lagged behind in development as compared with the rest of the body. Finally the larvae died before or soon after hatching.

15 $^{0}/_{00}$. At the time of the first inspection the Nauplius eye was not yet visible. Development took a normal course up to stage 3–4. From this stage on the yolk mass no longer diminished in the normal way and yolk cells began to show a granular structure. Compound eyes remained comparatively small. The experiment had to be broken off before the first zoea had hatched.

20, 25, 30, 35 and 40 $^0/_{00}$. The development took a normal course, leading to the appearance of normal zoeae.

45 $^0/_{00}$. At the time of the first inspection the eggs of one of the parent animals were found to be in a rather advanced stage of development (heart pulsations). Part of the eggs showed a normal development, which led to the appearance of normal zoeae; the rest showed some abnormalities (granular structure of yolk cells and head). Finally the parent animal died, after which the remaining eggs degenerated.

The eggs of the second parent animal proved to be in a very early stage of development at the time of the first inspection, no yolk-free part being as yet visible. At the time the experiment was broken off development had proceeded normally up to the appearance of the eye pigment.

Results

At a temperature of ca. 9° C a perfectly normal development of the eggs takes place in salinities ranging between 20–21 and 40–41 $^0/_{00}$. Possibly in some cases normal development may occur in salinities of 45 and 15 $^0/_{00}$. These salinities, however, are distinctly unfavourable.

Series 2a. Temperature 16–18° C. See fig. 3

The seawater concentrations used were 5–8, 10–13, 15–18, 20–23, 25–28, 30–33, 35–38 and 40–42 $^0/_{00}$. The wide salinity range in all experiments in this series is due to a considerable increase in concentration of the media as a result of evaporation.

5–8 $^0/_{00}$. Most of the eggs failed to develop because they were lost by the parent animal. The remaining ones showed abnormal development. Of the granular looking yolk cells only a small part was resorbed; the compound eye remained in-

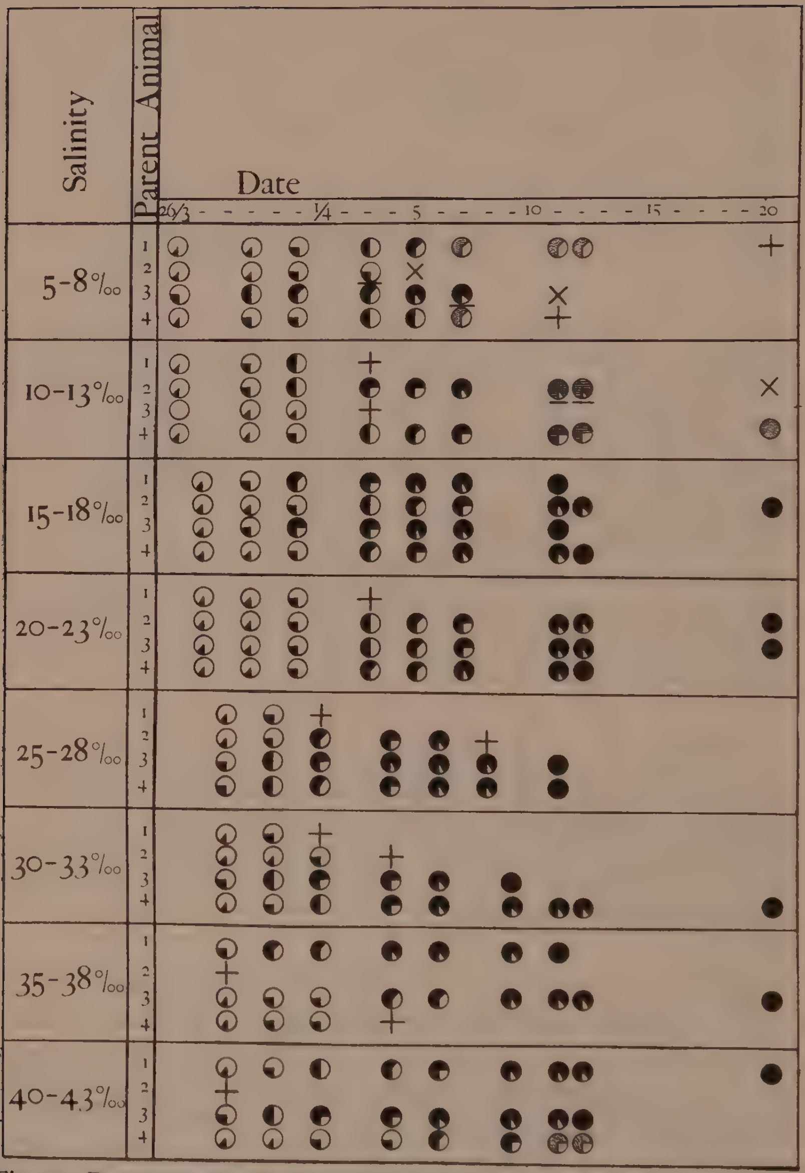


Fig. 3. Development of shrimp eggs in media of 5–8, 10–13, 15–18, 20–23, 25–28, 30–33, 35–38 and 40–42 ‰ salinity at a temperature of 16–18° C.

complete and most of the eggs were greatly swollen. None of the larvae hatched.

10–13 $^0/_{00}$. Here, too, a number of eggs were lost by the parent animals.

The development of the remaining eggs took a normal course up to the stage where the larvae were about to hatch. In this stage the eggs were lost by the parent animal. Another parent animal succeeded in keeping its eggs till development was complete; a considerable number of normal zoeae hatched. A small part of the eggs showed abnormal development (granular structure of yolk cells, compound eyes remaining undeveloped, abnormal size of heart).

15–18, 20–23, 25–28, 30–33, and 35–38 $^0/_{00}$. Normal development of the eggs, leading to hatching of normal larvae.

40–43 $^0/_{00}$. Most of the eggs developed normally; in some cases yolk resorption and development of the compound eye were retarded.

Results

At a temperature of 16–18° C a perfectly normal development of the eggs takes place in salinities ranging between 15–18 and 35–38 $^0/_{00}$. In salinities of 10–13 and 40–42 $^0/_{00}$ only part of the eggs developed normally.

Series 2b. Temperature 16–18° C. See fig. 4

Salinities at the beginning of the experiment: 10.2, 15.7, 20.3, 25.6, 30.7, 35.5, 40.5 and 45.3 $^0/_{00}$. During the course of the experiment all concentrations were renewed once. At the end of the experiment the salinities were: 11.3, 17.3, 22.1, 28.8, 33.5, 39.4, 44.8 and 51 $^0/_{00}$. Evaporation had therefore been quite considerable.

During the experiment 16 of the females died. Of these 3 belonged to the 10, 1 to the 15, 2 to the 20, 2 to the 25, 2 to the 35, 2 to the 40 and 4 to the 45 $^0/_{00}$ basin.

10.2–11.3 $^0/_{00}$. All females lost their eggs before development of the larvae was completed. The eggs of one of the females

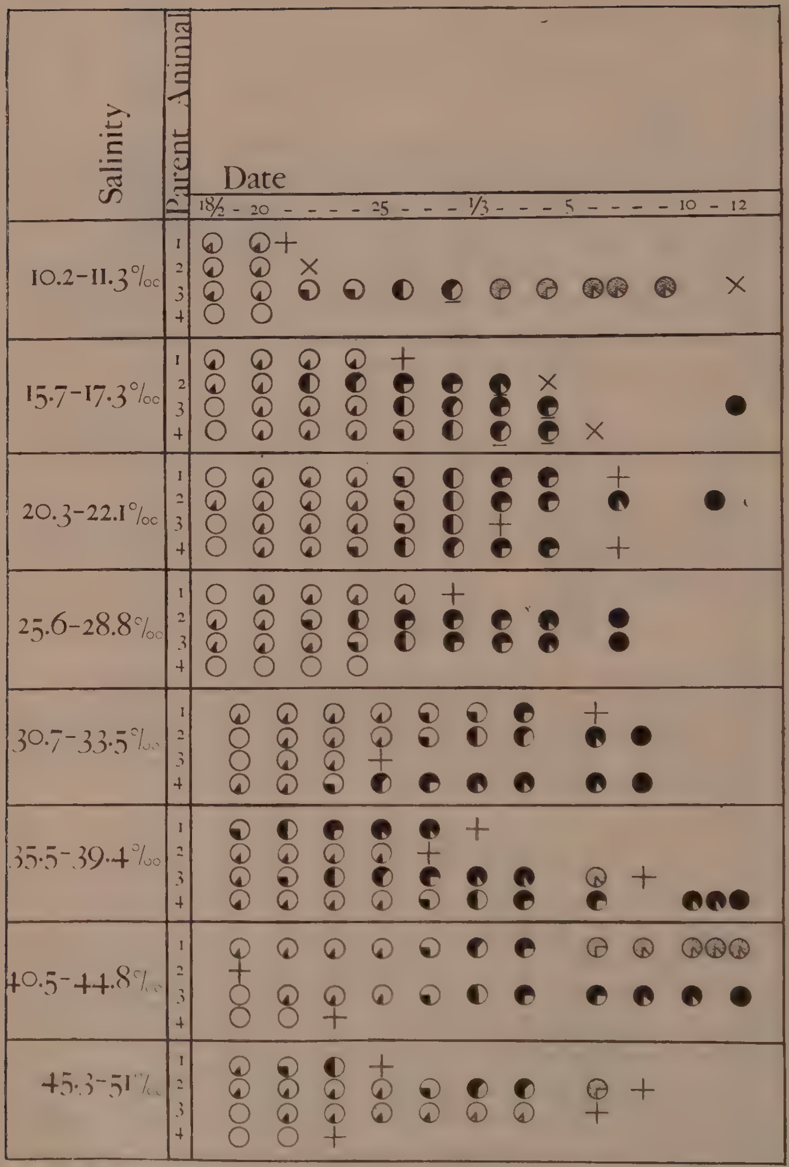


Fig. 4. Development of shrimp eggs in media of ca. 10, 15, 20, 25, 30, 35, 40 and 45 ‰ salinity at a temperature of 16–18° C.

reached the stage in which movements of the limbs could be observed; later on these movements ceased. Resorption of the yolk mass was retarded, the yolk cells showed a granular structure. None of the larvae hatched.

15.7–17.3 $^{0}/_{00}$. Here, too, almost all of the eggs were lost. The remaining eggs showed a normal development and finally a few normal larvae hatched.

20.3–21.1, 25.5–28.8, and 30.7–33.5 $^{0}/_{00}$. Normal development of the eggs, leading to the hatching of normal larvae.

35.5–39.4 $^{0}/_{00}$. Most of the eggs developed normally. The eggs of one of the parent animals showed some abnormalities. Later on this animal died.

40.5–44.8 $^{0}/_{00}$. Part of the eggs developed normally, the other part degenerated before hatching.

45.3–51 $^{0}/_{00}$. All eggs degenerated.

Results

Perfectly normal development took place in a range of salinities between 15–17 and 35–39 $^{0}/_{00}$. In a salinity of 40–45 $^{0}/_{00}$ only part of the larvae developed normally; below 15 $^{0}/_{00}$ no hatching took place.

The experiments 1, 2*a* and 2*b* are summarized in table 9. Its figures make it clear that, generally, the salinity range available for normal development of the eggs shifts in a downward direction with increasing temperature. It is further evident that normal development can take place in salinitites higher than 40 $^{0}/_{00}$. Considering that 35 $^{0}/_{00}$ is the highest salinity to be found in the North Sea this seems rather remarkable. On the other hand, development of the eggs in salinities lower than 16–20 $^{0}/_{00}$ only occurs in exceptional cases, whereas full-grown shrimps can be found in salinities even lower than 10 $^{0}/_{00}$! Thus, the salinity range available for the normal development of the eggs only covers the more saline part of the salinity range in which full-grown animals are able to live.

TABLE 9

Data concerning the development of shrimp eggs in media of different temperature and salinity

Temperature	Part of the eggs develop normally in a salinity of:	All eggs develop normally in a salinity of:	Part of the eggs develop normally in a salinity of:
8–10° C	ca. 15 $^0/_{00}$?	20.5–40.5 $^0/_{00}$	ca. 45 $^0/_{00}$
16–18° C (*a*)	ca. 11.5 $^0/_{00}$	16.5–36.5 $^0/_{00}$	ca. 41 $^0/_{00}$
16–18° C (*b*)		16–37 $^0/_{00}$	ca. 42.5 $^0/_{00}$

Particulars concerning distribution of egg-bearing females, together with data bearing upon time of the year and regions in which hatching of the larvae takes place, can be found in publications by HAVINGA (1930) and EHRENBAUM (1891). As these data are of interest in connection with my experiments a short summary of them is given here.

Ovigerous females occur throughout the year. Statistically, however, two main periods of spawning can be distinguished, one from the beginning of March to the end of June (summer eggs), the other covering the months of October and November (winter eggs). Owing to the difference in temperature the time required for development of the eggs is much longer for winter than for summer eggs. From his data HAVINGA calculates that at a temperature of ca. 9° C development of the eggs takes about 9 weeks, whereas at a temperature of 16° C only 30 days are required. In both cases about half of this time was required for the development of the eggs to the stage where the Nauplius eye becomes visible. Assuming this to be correct, HAVINGA's calculated figures for the total development of the eggs are in good agreement with the results of my rearing experiments. For instance, in my experiments at a temperature of 16° C (salinity 30 $^0/_{00}$) the time elapsing between the appearance of the Nauplius eye and hatching proved to be about 16 days. Consequently, the total development would have required about 32 days (HAVINGA found about 30 days). At a temperature of 9° C (salinity 25 $^0/_{00}$) hatching of the larvae took place about 32 days after the appearance of the Nauplius eye. Consequently total development would have taken about 64 days (HAVINGA found about 63 days).

Concerning the regions in which development and hatching of the larvae take place HAVINGA states that in zone I (see fig. 1) hatching of the larvae takes place both during summer and during winter, that in zone II females with ripe eggs only occur during the summer months, that in zone III ovigerous females may occur in the late summer, though their eggs do not develop, and that in zone IV no ovigerous females were ever found.

From the above it becomes clear that:

a. Generally, ovigerous females can only be found in the more saline part of the total area of distribution. The results of the rearing experiments, showing that development of the eggs is possible only in media of comparatively high salinity, agree with this observation.

b. With increasing temperature the development of the eggs takes place in media of lower salinity (HAVINGA's zone II). Salinity in this region amounts to about 20 $^0/_{00}$, temperature in April to 8–9° C. In my experiments at a temperature of 9° C a salinity of about 20 $^0/_{00}$ proved to be the lowest salinity limit for normal development of the eggs.

c. Later in the year egg-bearing females also occur in zone III. The salinity here is then 13–20 $^0/_{00}$, the temperature about 17° C. At this temperature the lowest salinity limit according to my experiments is about 15 $^0/_{00}$. That the eggs fail to develop in this area is possibly due to their being lost by the parent animal. In my experiments loss of the eggs frequently took place in low salinities, especially at high temperatures (16–18° C).

For comparison, the main data concerning the influence of temperature and salinity on egg development in *Ostrea*, *Carcinides* and *Crangon* are put together in table 10.

The table shows that the influence of temperature on the salinity limits is most distinct in *Carcinides* and *Crangon*. In both species the influence works in the same direction, at least as far as the lower limit is concerned. In the case of *Carcinides* the higher salinity limit was not appreciably affected by temperature, in the case of *Crangon* shifting of the higher as well as the lower salinity limit took place. Both limits shift in the same direction, upward with decreasing, downward with increasing temperature. In the case of *Ostrea* both limits expand with decreasing temperature, the lower salinity limit accordingly shifting in a direction opposite to that recorded in *Crangon* and *Carcinides*. The

TABLE 10

Influence of temperature on the salinity limits for egg development in *Carcinides*, *Ostrea* and *Crangon*.

	temperature (degrees C)	lower salinity limit* (in $^0/_{00}$)	higher salinity limit* (in $^0/_{00}$)
Carcinides	10	26	40
	16	20	40
Ostrea	16	6	37
	23–26	8	36
Crangon	9	18	45
	17	12	42

(*) The salinity limits represent the highest or the lowest salinity in which normal development of the eggs can take place; that is to say, salinities in which normal as well as abnormal development were recorded.

possibility still remains that this discrepancy can be explained in the way which was suggested by BROEKHUYSEN (see page 37), although this does not seem very probable in view of the fact that the experiments with full-grown shrimps point in the opposite direction.

Finally, the question remains whether differences in salinity have any influence on the rate of development of the eggs. According to BROEKHUYSEN (p. 97) development of *Carcinides* eggs is neither accelerated nor retarded by differences in salinity. On the other hand, AMEMIYA found that in *Ostrea gigas* development of the eggs is considerably retarded in extremely high and extremely low salinities. Though in my experiments with *Crangon* the influence of salinity on the rate of development of the eggs proved to be rather small, this influence, as shown in table 11, is not altogether negligible.

In the table the average number of days elapsing between the appearance of the Nauplius eye and the beginning of the first larval movements is recorded for a number of cases, each case referring to a given temperature and salinity. The average was taken from 1–4 groups of eggs, each group belonging to a different parent animal, the number of which is recorded in a special column. Eggs belonging to different parent animals only showed minor differences in rate of development.

On the whole, development is slightly retarded in low salinities. The same influence, although to a smaller

TABLE 11

Rate of development of shrimp eggs in relation to temperature and salinity

Series 1. Temp. 8–10° C			Series 2*a*. Temp. 16–18° C			Series 2*b*. Temp. 16–18° C		
salinity in $^0/_{00}$	average number of days	number of parent animals	salinity in $^0/_{00}$	average number of days	number of parent animals	salinity in $^0/_{00}$	average number of days	number of parent animals
10 –11			5–8	10	1	10 –11	12	1
15.5–16.5	23	1	10–13	11	2	15.7–17.3	9	1
20 –21	15	3	15–18	8	4	20.3–22.1	9	1
25 –26	17	1	20–23	10	3	25.5–28.8	9	2
30 –31	16	1	25–28	8	3	30.7–33.5	6.5	2
35 –36	11	3	30–33	8	2	35.5–39.4	10.5	2
40 –41	11	2	35–38	8.5	2	40.5–44.8	9	2
45 –46			40–42	10.5	2	45.3–51		

degree, is exercised by extremely high salinities. The highest rate of development was recorded in salinities of 35–41 $^0/_{00}$ at a temperature of 8–10° C and in salinities of 25–33 $^0/_{00}$ at 16–18° C. The retarding influence exercised by a too low salinity is much more distinct at a high than at a low temperature. Table 11 at the same time shows that at a temperature of 16–18° C the development proceeds 1$\frac{1}{2}$–2 times as quickly as at a temperature of 8–10° C.

The difference appears to be greatest in salinities lower than 30 $^0/_{00}$. The conclusions drawn from the data compiled in table 11 must be regarded as provisional, however, the number of data being too small to permit of any well founded inference.

Summary of part I

1. The salinity optimum for shrimps of about 2 years old is ca. 33 $^0/_{00}$ at a temperature of 3–5° C, and 28–29 $^0/_{00}$ at 20–22° C. In other words: with increasing temperature the salinity optimum shifts towards the less saline water.

2. The salinity optimum for shrimps of about one year old at a temperature of 22° C is 18–19 $^0/_{00}$. Consequently, with increasing age the optimum shifts towards a higher salinity.

3. A combined influence of temperature and salinity in the same sense as stated sub 1 could also be demonstrated in the case of newly hatched larvae; here, too, increasing temperature caused the salinity optimum to shift in a downward direction.

4. The salinity range available for normal development of the eggs proved to depend on temperature in a similar way as described sub 1 and 2, the higher as well as the lower salinity limit shifting downward with increasing temperature.

5. The salinity range for a normal development of the eggs proved to be very wide. It includes not only the more saline part of the salinity range of full-grown shrimps in nature, but also higher salinities up to 40 ⁰/₀₀, i.e. 4–5 ⁰/₀₀ more than we find in their natural habitat.

6. The above-mentioned results agree with data collected by Havinga concerning:

a. distribution of young and full-grown shrimps,

b. seasonal migration,

c. salinities in which development of the eggs takes place in nature.

Various statements in literature concerning distribution and migration in a number of Crustacea make it clear that in this respect *Crangon* is no isolated instance. For a detailed account I refer to a paper by Balss (1930), from which the following is quoted:

"Bei den marinen Formen sind sie (die Wanderungen) besonders aus der gemässigten Zone bekannt, und erfolgen so, dass die Tiere im Sommer ins oberste Litoral gehen, wo die Temperaturen höher sind, während sie im Winter, wenn die Oberflächentemperaturen niedriger und stark wechselnd sind, sich mehr in die Tiefe (etwa 40 m) mit ihrer wärmeren und gleichmässigeren Temperatur zurückziehen." These general conclusions are based on data concerning the following species: *Leander adspersus*, *Homarus vulgaris*, *Homarus americanus*, *Cancer pagurus*, *Callinectes sapidus*, *Pandalina brevirostris*, *Galathea squamifera*, *Chionoecetes opilio*, *Maja squinado*, *Portunus puber*, *Carcinides maenas* and *Eriocheir sinensis*. In all these cases a seasonal change in distribution occurs, essentially similar to that described for *Crangon* and *Carcinides*. Possibly in these cases, too, a combined influence of temperature and salinity could be demonstrated.

BALSS also compiles the available data as to the area where the eggs develop in nature. In the following cases development only takes place in the more saline part of the area of distribution: *Carcinides maenas* (see also BROEKHUYSEN 1936), *Crangon crangon*, *Pandalus montagui*, *Leander adspersus*, *Homarus americanus*, *Cancer pagurus*, and *Callinectes sapidus*. It should be added that even in some fresh water Crustacea development of the larvae takes place in the sea; to this end the parent animals migrate to the sea in order to spawn (e.g. *Eriocheir sinensis* and *Leander longirostris*).

PART II. THE INFLUENCE OF TEMPERATURE AND SALINITY ON THE OSMOTIC BEHAVIOUR OF THE SHRIMP

Introduction

The experiments described in part I prove that for *Crangon* the suitability of a given medium depends largely upon its temperature-salinity conditions. Obviously these two factors act in combination. This brings us immediately to the next question: how does this combined influence of temperature and salinity come about?

The most plausible suggestion seemed to me that temperature has some influence or other on the osmotic behaviour of the shrimp. Distributional data make it abundantly clear that *Crangon* is a pre-eminently euryhaline species, occurring over a salinity range between approximately 10 and 35 $^0/_{00}$. Besides, distributional data show that the greater part, if not the whole of the range is covered twice a year by each individual. As far as I could make out nothing is known about the way in which the internal concentration is influenced by these drastic changes in external concentration, but, a priori, there are two possibilities:

1. all changes in concentration of the external medium are followed passively by the internal medium; in other words the animal is perfectly poikilosmotic;
2. the shrimp disposes of osmoregulatory mechanisms which enable it to maintain an internal concentration more or less independent of the external concentration.

The object of the experiments to be described in the following section can be summarized as follows.

In the first place: which of these two possibilities is realized in *Crangon*? In other words: does *Crangon* dispose of the capacity of active osmoregulation?

In the second place (in case active osmoregulation could be proved to exist): what is the influence of temperature on the osmoregulatory processes?

Literature is here only dealt with in so far as the influence of temperature on the osmotic behaviour of Crustacea is concerned. For data concerning osmoregulation in Crustacea in general I refer to KROGH's recent monograph, which gives a detailed account of the subject.

WIDMANN (1935) proved the existence of periodical changes in blood concentration in a number of Amphipoda, Isopoda and Decapoda. These changes always appear to take place in spring and autumn. During autumn the osmotic concentration of the blood appears to increase gradually, reaching a maximum during the winter months. Towards spring the osmotic blood concentration decreases to a minimum value, which is maintained throughout the summer. These conclusions bear on the following species: *Eriocheir sinensis* and *Potamobius astacus* (Decapoda), *Gammarus marinus*, *G. pulex*, *Orchestia gammarellus*, *Talitrus saltator* and *Ligia oceanica* (Amphipoda), *Asellus aquaticus*, *Oniscus asellus*, *Porcellio scaber*, *P. dilatatus* and *Armadillidium cinereum* (Isopoda). These species, at least as far as they are aquatic, all proved to be hypertonic in respect to the media in which they were kept. For *Porcellio scaber* it could be proved experimentally that the seasonal changes in blood concentration are caused solely by periodical changes in temperature: animals which were kept under an extremely low temperature during winter showed an increase in freezing point depression surpassing the normal increase by 0.14° C.

OTTO (1934) states that specimens of the small crab *Heteropanope tridentata* reacted on a temporary increase of the room temperature by lowering the osmotic blood concentration. At the same time this increase in temperature caused the death of a great number of specimens. The first to die were the animals kept in tap water; they were followed by the animals kept in brackish water. In more saline water, finally, nearly all animals remained alive. This latter observation is of interest in connection with the results of part I. In the case of *Heteropanope* an increase of temperature could apparently be better endured when the concentration of the external medium was relatively high, whereas *Crangon* behaved in just the opposite way. Like *Crangon*, *Heteropanope* is pre-eminently euryhaline, and, according to OTTO, hypertonic in respect to the surrounding medium.

For young specimens of *Eriocheir*, kept in fresh water, OTTO (1937) states that in this case, too, an increase in temperature caused a decrease in osmotic concentration of the blood. This phenomenon could be followed in a number of individuals, each of which was kept for some time in temperatures of 4, 24 and 4° C successively. All individuals showed a decrease in osmotic concentration of the blood after the change from 4 to 24° C.

Subsequent lowering of the temperature from 24 to 4° C caused an increase of the blood concentration in three cases out of six; in the remaining three cases no change took place.

OTTO (1937) further gives some observations concerning the influence of temperature upon the rate at which adaptation of the blood takes place after the external concentration has been changed. The rate of adaptation appeared to be somewhat greater at a temperature of 23° C than at 13° C.

FRITSCHE (1917), in his study on *Daphnia magna*, states that the internal concentration is comparatively low in animals which are kept at extremely high or at extremely low temperatures. A maximum internal concentration was found at temperatures between 10 and 20° C. Differences, however, were only small, and KROGH (1939) doubts whether they are of any significance statistically. *Daphnia magna*, too, proved to be hypertonic in respect to the surrounding medium.

MARGARIA (1931) states for *Maja squinado* and *Portunus depurator* that at a higher temperature the blood adapts itself more quickly to a changed external concentration than at a lower one.

BATEMAN (1933), determining the blood concentration of *Carcinides maenas* at temperatures of 2.3 and 15.7° C, found very small differences only; at a temperature of 15.7° C the blood concentration appeared to be slightly less than at 2.3° C.

DRILHON-COURTOIS (1934), using the method of quantitative chemical analysis, states that in *Telphusa* (*Potamon*) *fluviatilis* the composition of the blood shows a few seasonal differences. During autumn the Na, Ca and especially the K content of the blood proved to be considerably higher, the P and protein content somewhat lower than during spring.

CHAPMAN (1928) states that in hibernating insects the blood often shows an increased concentration during the winter months; in some cases the increase was caused by the transition of free water into colloid-bound water. The ecological significance of this phenomenon was supposed to lie in an increased resistance to freezing.

In connection with the experiments to be related here the results of WIDMANN and OTTO are of special interest. These results can be summarized as follows:

A number of decapod and other Crustacea, all without exception hypertonic in respect to the surrounding medium, reacted on an increase in temperature by a decrease in osmotic concentration of the blood. In other words, an increased temperature caused the difference in concentration between external and internal medium to decrease.

A. METHOD

The method I used in order to determine the concentration of the internal and external medium consisted in measuring the specific conductivity, or rather the specific resistance of these fluids. The apparatus used for this purpose was obtained from the N.V. Philips (Eindhoven), who sells it under the name of "Philoscop". The apparatus acts on the principle of the bridge of Wheatstone, measuring an unknown resistance in terms of a known (standard) resistance.

As an indicator for adjustment of the measuring bridge a cathode ray tube is used. The fluid to be measured is contained between the electrodes of a measuring cell. In order to prevent polarisation the bridge part of the Philoscop is fed with an alternating voltage of 1000 c/s, delivered by a low frequency oscillator (Philips, type G.M. 4260). The measuring voltage amounts to about 2 volts, so that during a determination practically no increase of temperature occurs.

The measuring accuracy amounts to about 0.1%. This degree of accuracy can be reached by making use of the Philoscop in combination with a series of separate standard resistances. The deviation of the unknown resistance can be read in tenths of percents with the aid of a special dial extending from + 25 to — 20%.

The measuring cell consists of two vertically mounted platinum electrodes, the inner surfaces of which are covered with a thin coating of platinum black. The size of each electrode is about 1 cm^2, the distance between them 1 cm. The platinum conducting wires are each enclosed in a narrow glass tube. They are externally connected to the two terminals on top. The whole structure (electrodes and wires) is enclosed in a glass casing. In order to fix the distance between them the electrodes are fused with two glass plates of the same size, the glass plates being held in position by two transverse glass connections.

By multiplying the resistance measured between both terminals with a constant factor the specific resistance of a given fluid can be calculated. This factor, the value of which depends upon the geometrical properties of the electrodes, can be determined by checking the cell in a fluid of known specific resistance. During the period of time in which the experiments took place the multiplying factor of my measuring cell was determined at regular intervals; it remained the same throughout this period, which proves that no changes took place in either size or structure of the electrodes.

Since the total amount of blood which can be taken from a full-grown shrimp generally varies between about 50 and 200 mg only it was necessary to work with very small amounts of fluid. The quantity required for immersing the cell was about 10 cc. By making some alterations in its construction I was able to reduce this amount to 4–5 cc. [1]) To this end the lower part of the casing was cut off somewhat above the platinum electrodes; the remaining part was provided with a ground outer surface corresponding to the ground inner side of a small glass jar. The latter was destined to hold the fluid to be measured (see fig. 5). It follows from the above, however, that the blood still had to be diluted 25–100 times in order to yield a quantity of fluid sufficient for one determination. Originally, I had the intention always to use exactly the same degree of dilution. The conductivity values found would thus have been directly comparable with each other. The following difficulties, however, made it practically impossible to use this method:

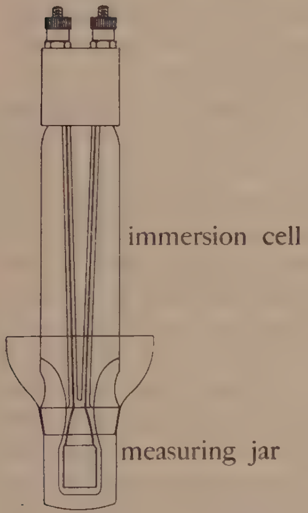


Fig. 5. Measuring cell and jar.

a. The quantity of blood which can be taken from one shrimp shows great individual variations, being largely dependent on the size of the animal, its physiological condition (moulting!), and on the salinity of the external medium. By fixing the amount of blood necessary for one determination on e.g. 70 mg a number of animals would have to be rejected on account of shortage of blood. Since the animals, before being used, had often been submitted to a prolonged treatment in media of a given temperature and salinity the rejection of a number of animals would have involved a considerable loss of time.

b. It proved by no means easy to obtain and to measure with the necessary degree of exactitude a definite and very small quantity of blood. Anyhow, I failed to find a simple and quick method for doing this.

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[1]) In the meantime a measuring cell suitable for determinations on still smaller quantities of fluid has been constructed by the N.V. PHILIPS.

These difficulties compelled me to leave the principle of using a fixed degree of dilution.

The procedure I finally adopted ran as follows:

Some time before a series of determinations was to be carried out a number of 20 cc weighing bottles were steamed for about 20 minutes over boiling distilled water. This treatment is necessary in order to prevent the glass from giving off ions, thereby influencing the conductivity of the fluid to be measured. After that, bottles and stoppers were carefully dried with clean filter paper (SCHLEICHER and SCHÜLL no. 595). Thereupon, one of the bottles was filled with ca. 12 cc of twice distilled water, the exact weight of which was determined to tenths of milligrams on a sensitive scale. Next, 50–70 mg of blood (resp. seawater) was added to the solvent, after which the whole (solvent + blood + bottle) was weighed again. The degree of dilution thus having been determined exactly the resistance of the solution was measured.

All resistance (resp. conductivity) determinations were carried out at a temperature of exactly 20° C. To this end the bottles were placed in a thermostat, the water in which was stirred continually. Before making a determination the bottle in question was thoroughly shaken in order to obtain an equal distribution of the solved material. Thereupon, ca. 2 cc of the solution were quickly decanted in the measuring jar, which had been thoroughly cleansed beforehand. This quantity of fluid was used for rinsing the electrodes. After removal of the rinsing fluid the jar was filled again, now with 5 cc of the solution, and the electrodes were put into position. The whole was left in the thermostat for two minutes, after which the resistance was read. The remaining 5 cc, after being thoroughly shaken again, were used for a second determination.

Since a different degree of dilution was used for each determination the results could only be compared after a compensatory calculation. To this end the specific conductivity of the undiluted blood was calculated from the available data, viz:

1. specific resistance of the diluted blood (y),
2. specific resistance of the solvent (z),
3. degree of dilution (a).

Assuming the resistance of the undiluted blood to be x (specific conductivity $\frac{1}{x}$) the following equation holds good:

$$\frac{1}{x \cdot a} + \frac{1}{z} = \frac{1}{y}$$

($\frac{1}{x \cdot a}$ stands for the specific conductivity of the blood diluted a times, without taking in account the conductivity of the solvent).

Accordingly, $x = \frac{z \cdot y}{a\,(z-y)}$

Treated this way, the results of all determinations are directly comparable to each other.

For the sake of convenience all results were multiplied by 1000. The conductivity values thus obtained are comparable to, though by no means identical with, specific conductivity values for the undiluted blood expressed in reciprocal Ohms. They are not identical, because no allowance was made for the fact that by diluting the blood the dissociation is considerably increased. The calculated conductivity value in reality represents the specific conductivity of the undiluted blood, assuming the degree of dissociation to be the same as in the blood diluted a times. Consequently, the results only have relative value, but the degree of dilution being of the same order throughout the experiments they can be compared among each other, which is sufficient for our purpose. This consideration also made me refrain from multiplying all results by the "multiplying factor".

Use of the unit "reciprocal Ohms" not being justified here I expressed all conductivity values in "conductivity units" (C.U.).

Concerning the exactitude of the method three limiting factors have to be taken into account.

1. The measuring accuracy of the apparatus.

By making use of the "%-dial", combined with a series of separate standard resistances, the measuring accuracy amounts to 0.1 % of each resistance to be measured.

2. The variability in conductivity of the solvent.

The conductivity of the solvent (twice distilled water) partly depends upon the amount of CO_2 absorbed from the air.

Generally, variations of ca. 10 % were recorded in subsequent determinations on the same sample. The influence of this variable factor on the exactitude of a determination can be calculated for each separate case. The calculation is carried out below for seawater concentrations of 15 and 45 $^0/_{00}$ diluted 200 times, 15 and 45 $^0/_{00}$ representing the limits of the concentration range occurring in my experiments.

a. The specific resistance of 45 $^0/_{00}$ seawater diluted 200 times amounts to ca. 2350 Ω, the specific conductivity to 4.3×10^{-4} reciprocal Ω.

A difference in conductivity of 0.1 % (the minimum difference the apparatus is able to measure) in this case amounts to 4.3×10^{-7} rec. Ω. The specific conductivity of the twice distilled water I used amounted to ca. 2×10^{-6} rec. Ω, with a variability of 10 % or 2×10^{-7} rec. Ω.

Thus, a measured difference of 4.3×10^{-7} rec. Ω does not necessarily mean that in reality the difference in conductivity between the two solutions amounted to 0.1 %, for it might just as well have been 2×10^{-7} rec. Ω (or 0.05 %) more or less than 0.1 %, i.e. 0.05 or 0.15 %. In other words, at this concentration only differences greater than 0.15 % can be considered significant.

b. The specific conductivity of 15 $^0/_{00}$ seawater diluted 200 times amounts to 1.5×10^{-4} rec. Ω. A difference of 0.1 % in this case amounts to 1.5×10^{-7} rec. Ω. As we saw that the variability in conductivity of the solvent was about 2×10^{-7} rec. Ω only differences greater than 3.5×10^{-7} can be considered significant. This difference represents about 0.25 % of the value found for the specific conductivity of the 15 $^0/_{00}$ seawater.

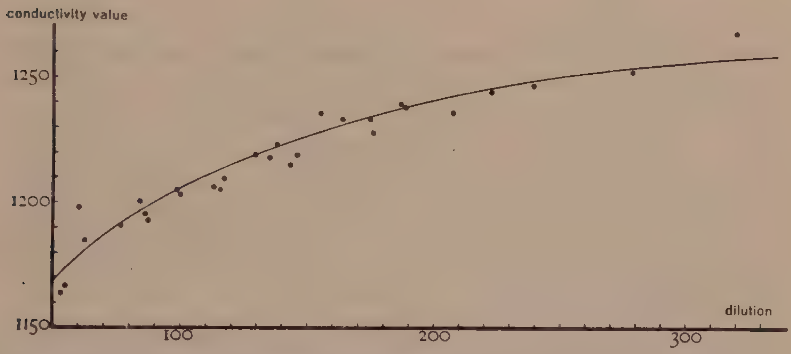
3. The degree of dilution.

In determining conductivity values I made use of dilutions ranging between 150 and 200 times. This is justified only when it can be safely assumed that at a dilution of 150 times complete dissociation has taken place, so that a further dilution involves no change in molecular conductivity. In order to examine this the relation between the conductivity value and the degree of dilution was recorded for a sample of 35.3 $^0/_{00}$ seawater. The result is given in graph 19.

It is evident that a dilution of 150 times is not yet sufficient to obtain complete dissociation: further dilution up to 200 times results in an increase of the conductivity value of 1.2 % (from 1225 to 1240 C.U.).

Summarizing, we come to the following conclusions.

The measuring accuracy of the apparatus and the variability in conductivity of the solvent permitted an exactitude of at least 0.25%. In addition an allowance of 1.2% has to be made for differences which arise from the variations in the degree of dilution. A further allowance has to be made for small sources of error, viz. the release of ions by the glassware, evaporation of the solvent, small temperature fluctuations and insufficient rinsing of the electrodes. Consequently, the degree of accuracy may be estimated at 1.5–2%, this figure referring to determinations of blood or seawater of a concentration of ca. 35 $^0/_{00}$.



Graph 19. Relation between the degree of dilution and the conductivity value for a sample of 35.3 $^0/_{00}$ seawater.

For concentrations lower than 35 $^0/_{00}$ the degree of accuracy is somewhat greater, the influence of a varying degree of dilution being smaller in this case. For concentrations higher than 35 $^0/_{00}$ the degree of accuracy is somewhat less.

By using a dilution of at least 300 times the differences arising from the use of a varying degree of dilution would of course be greatly reduced. However, making the degree of dilution greater than 200 times seemed inadvisable, since by doing so the influence of other variable factors would considerably increase, e.g. the influence of the variable conductivity of the solvent, the influence of ions released by the glassware, etc.

In order to test the accuracy of the method I made several determinations of the conductivity value of a sample of 35 $^0/_{00}$ seawater, making use of dilutions of 150 to 200 times.

The following results were obtained:

dilution	conductivity value (C.U.)
155	1235
164	1233
175	1233
176	1228
187	1239
189	1238

The difference between the extreme values amounts to less than 1 %.

The collecting of the blood was carried out by sucking it up into a piece of glass tubing, one end of which was drawn out to form a capillary. The other end, after being greased, was connected with a rubber tube closed at the end. By slowly drawing back the rubber tube the required amount of blood could be sucked into the capillary.

The capillaries used for collecting the blood always were carefully rinsed with distilled water. They were dried by treating them with aceton and ether subsequently. Each capillary was only used once. The glass tubing from which they were made had never been used before.

Some time before the collecting of the blood was to take place the animal in question was wrapped in a soft towel in order to remove the adhering seawater as completely as possible. The capillary was then brought laterally under the carapace, and, by piercing the skin, one of the blood lacunes was reached. At this moment a small quantity of blood entered into the capillary, after which the rubber tube was slowly pulled up.

In a few cases the blood appeared to be mixed with the contents of the intestine, but this could easily be recognized by the dark colour of the fluid thus collected. Samples like these were not used for determinations.

B. EXPERIMENTS

I. Determination of the individual differences in blood concentration in a number of shrimps kept under the same external conditions.

Twelve shrimps were kept for 6 days in a salinity of 30 $^0/_{00}$, at a temperature of 8° C. At the end of this period individual conductivity values amounted to 837, 856, 875, 878, 885, 888, 901, 915, 920, 921 and 943 C.U. These figures make it clear that a determination on one single animal is of little value. Therefore, in examining blood concentrations under various external conditions I always determined the concentration of a number of animals individually, in most cases 10.

II. Preliminary determinations.

This series was carried out in order to gain a general insight into the osmotic behaviour of the shrimp, and to determine the number of days necessary for a complete adaptation of the blood to changed external concentrations.

A number of shrimps, which had been kept in a salinity of 30 $^0/_{00}$ at a temperature of 8° C, were distributed over 4 degrees of salinity (15, 25, 35 and 45 $^0/_{00}$), temperature remaining the same. Transfer of the animals in the various salinities was carried out gradually over 2–3 days. Two days after the transfer was completed conductivity determinations were started. Every other day the blood of 4 specimens (one from each salinity) was examined. The experiment lasted for 20 days. The results are put together in table 12.

From this table it appears that the shrimp is able to maintain a certain difference in concentration between the internal and the external medium. However, no complete independence between blood concentration and external concentration exists, the internal concentration following to some extent the concentration of the external medium. In salinities lower than ca. 23 $^0/_{00}$ the blood is hypertonic, in those higher than ca. 23 $^0/_{00}$ the blood is hypotonic in respect to the external concentration. The hyper- or hypotonicity increases as the distance to the point of isotonicity becomes greater.

It further appears that in each of the salinities the blood reaches a stable condition about 2 days after the transfer of the animals took place. In the following 16–20 days no essential changes in blood concentration were recorded.

The animals marked with an asterisk were examined shortly after moulting. In these cases the difference in concentration between internal and external medium proved to be considerably smaller than in specimens with a hard exoskeleton.

TABLE

Conductivity of the blood in single animals, 2–20 days after

	± 15 $^0/_{00}$			± 25 $^0/_{00}$		
days after transfer	conductivity of blood	conductivity of medium	salinity of medium	conductivity of blood	conductivity of medium	salinity of medium
2	629 C.U.	530 C.U.	14.98 $^0/_{00}$	988 C.U.	875	25.26 $^0/_{00}$
4	669	528		828	873	
6	664	534	15.00 $^0/_{00}$	864	883	25.16 $^0/_{00}$
8	701	525		862	862	
10	696	533		840	862	
12	564*	540		814	867	
14				869	866	
16	696	537	14.99 $^0/_{00}$	873	873	25.25 $^0/_{00}$
18				845	876	
20				799*		

III. Influence of temperature on the concentration of the blood in media of various salinities.

The experiments described in part I led to the assumption that in the shrimp the osmotic behaviour is affected in some way or other by temperature. This assumption was supported by the investigations of Otto and Widmann, dealing with the influence of temperature on the osmotic concentration of the blood in a number of Crustacea.

The species examined by Otto and Widmann all proved to be hypertonic in respect to the media in which they were examined. The degree of hypertonicity appeared to decrease with increasing temperature. In the case of *Crangon* hypertonicity makes place for isotonicity at a comparatively low external concentration (ca. 23 $^0/_{00}$). In concentrations higher than ca. 23 $^0/_{00}$ the blood remains definitely hypotonic.

It was my intention to study the influence of temperature on the concentration of the blood both in the hypertonic and the hypotonic condition. To this end a number of full-grown shrimps were kept in two series of salinities (15, 25, 35 and 45 $^0/_{00}$) under the same conditions as described on page 7. The series were kept at temperatures of 3–5 and 22° C respectively.

In order to provide ample time for acclimatisation the animals were left for one week in each of the salinities. After that,

2

ransfer in media of various salinities. Temperature 8° C

± 35 $^0/_{00}$			± 45 $^0/_{00}$		
onductivity of blood	conductivity of medium	salinity of medium	conductivity of blood	conductivity of medium	salinity of medium
1105 C.U.	1192 C.U.	34·76 $^0/_{00}$	1309 C.U.	1508 C.U.	45·17 $^0/_{00}$
943	1176		1236	1488	
933	1178	34·47 $^0/_{00}$	1313	1518	44·70 $^0/_{00}$
1029	1163		1235	1502	
1007	1175		1321	1518	
858	1190		1605*	1522	
1033	1179		1309	1511	
975	1182	34·49 $^0/_{00}$	1226	1518	44·67 $^0/_{00}$
1039	1167		1195	1538	
1041	1174		1304	1508	

the blood concentration of at least 11 animals out of each salinity was determined. The results, which are put together in table 13, are charted in graph 20, together with data contained in the tables 14 and 15.

The data make it clear that in *Crangon*, like in the species investigated by OTTO and WIDMANN, the osmotic behaviour is influenced by temperature. In external media of 25, 35 and 45 $^0/_{00}$ the blood concentration proves to be highest at a temperature of 3–5° C. In a medium of 15 $^0/_{00}$, on the other hand, the highest blood concentration is recorded at a temperature of 22° C. In other words, the difference between internal and external concentration is greater at high than at low temperatures. This applies both to cases where the blood is hypertonic and to cases where it is hypotonic in respect to the external medium. So far as they can be compared these results are exactly opposite to those obtained by OTTO and WIDMANN with a number of other Crustacea. They found the difference between internal and external concentration to be greater at low than at high temperatures.

The data represented in table 13 do not at first sight suggest an obvious explanation for the combined action of temperature and salinity as described in part I. Considering that a more

TABLE 13

Conductivity of the blood in media of various salinities at temperatures of 4 and 20–22° C respectively

4° C

external medium		internal medium		
salinity in $^0/_{00}$	conductivity in C.U.	average conductivity in C.U.	number of animals	standard deviation $\left(\sqrt{\frac{\Sigma V^2}{n-1}}\right)$ in C.U.
15.72	569	643	12	47
25.17	889	837	13	29
35.16	1232	983	13	21
44.70	1591	1324	13	35

20–22° C

external medium		internal medium		
salinity in $^0/_{00}$	conductivity in C.U.	average conductivity in C.U.	number of animals	standard deviation $\left(\sqrt{\frac{\Sigma V^2}{n-1}}\right)$ in C.U.
15.30	560	656	13	25
25.20	895	767	13	24
35.34	1250	968	13	32
44.90	1568	1285	11	63

detailed knowledge of blood concentrations at various temperatures and salinities would possibly furnish some point of contact with the previously collected data I decided to fill the gaps between the determinations already made with a new series of determinations.

In the first place it seemed of interest to examine blood concentrations under the temperature-salinity conditions experimentally found to be optimal, that is to say, in salinities of about 29 and 33 $^0/_{00}$, at temperatures of 20–22 and 3–5 ° C respectively. In the second place I wanted to get a better insight into the osmotic behaviour in the neighbourhood of the point of isotonicity. A series of determinations around this point could possibly serve to give the provisionally adapted rule—greater differences between internal and external medium at higher temperatures—a more sound foundation.

These considerations induced me to determine the blood concentration in four series of animals kept in the following media for at least 4 days: 2 series around the optimum (salinities 27, 29, 31 and 33 $^0/_{00}$) and 2 around the point of isotonicity (salinities 17, 19, 21 and 23 $^0/_{00}$), both pairs at temperatures of 3–5 and 20–22° C respectively.

The results of these determinations can be found in the tables 14 and 15 (see also graph 20).

The joint data of these tables, together with those of table 13, give a fairly complete picture of the dilution curves of the blood at different temperatures, in so far as external concentrations between ca. 35 and ca. 15 $^0/_{00}$ are concerned. They are re-

TABLE 14

Conductivity of blood in salinities ranging between 27 and 33 $^0/_{00}$ at temperatures of 3–5 and 20–22° C respectively

3–5° C				
external medium		internal medium		
salinity in $^0/_{00}$	conductivity in C.U.	average conductivity in C.U.	number of animals	standard deviation $\left(\sqrt{\frac{\Sigma V^2}{n-1}}\right)$ in C.U.
26.92	1000	870	10	19
28.91	1027	896	9	27
31.00	1104	939	9	28
32.61	1164	954	10	37

20–22° C				
external medium		internal medium		
salinity in $^0/_{00}$	conductivity in C.U.	average conductivity in C.U.	number of animals	standard deviation $\left(\sqrt{\frac{\Sigma V^2}{n-1}}\right)$ in C.U.
27.12	945	817	9	20
28.78	1014	843	8	24
30.97	1096	911	8	28
33.30	1169	940	9	42

TABLE 15

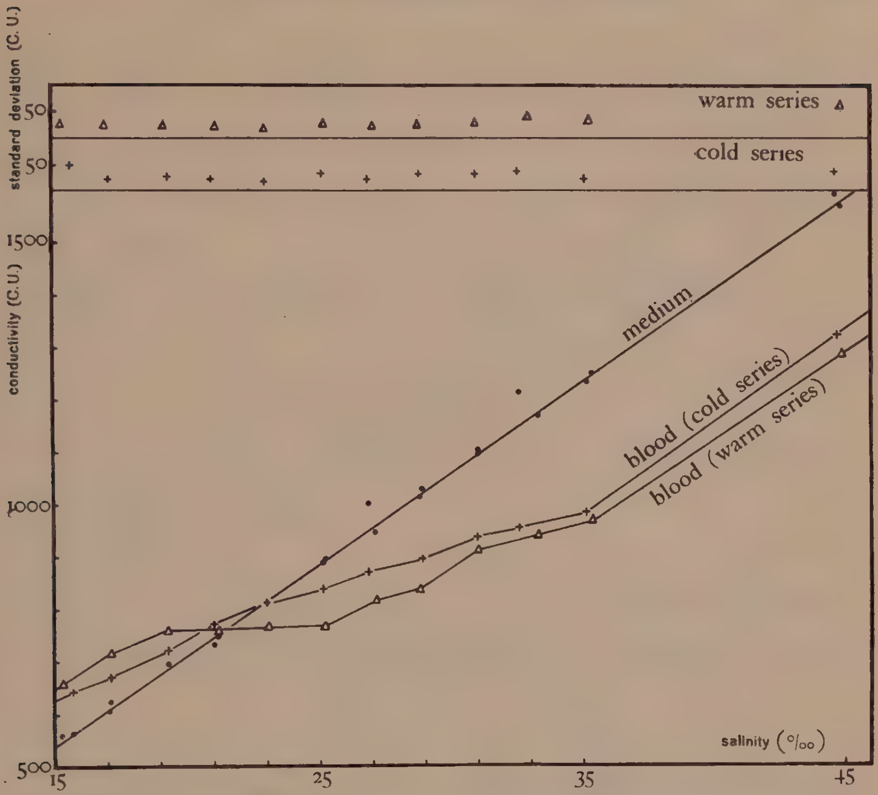
Conductivity of blood in salinities ranging between 17 and 23 $^0/_{00}$, at temperatures of 3–5 and 20–22° C respectively

3–5° C				
external medium		internal medium		
salinity in $^0/_{00}$	conductivity in C.U.	average conductivity in C.U.	number of animals	standard deviation $\left(\sqrt{\frac{\Sigma V^2}{n-1}}\right)$ in C.U.
17.12	622	672	9	20
19.29	695	722	9	24
20.97	727	773	8	19
22.94	818	814	10	13
20–22° C				
external medium		internal medium		
salinity in $^0/_{00}$	conductivity in C.U.	average conductivity in C.U.	number of animals	standard deviation $\left(\sqrt{\frac{\Sigma V^2}{n-1}}\right)$ in C.U.
17.05	605	714	10	25
19.24	692	757	9	24
21.13	746	758	8	20
22.99	814	766	7	16

presented graphically in graph 20. Graph 20*b* gives a smoothed representation of the same graph, obtained via graph 20*a*. This figure itself has been obtained by plotting the hyper- and hypotonicity resp. at temperatures of ca. 4 and ca. 20° C against the salinity of the external medium.

The following two points should be noted:

1. The course of the dilution curves for the blood appears to be different for high and low temperatures. The angle under which the dilution curve for the blood meets the dilution curve for the external medium is greater at a high than at a low temperature. Accordingly, the difference between the blood concentrations at high and at low temperature is relatively great in external salinities directly adjoining the point of isotonicity.



Graph 20. Conductivity of blood in salinities ranging between 15 and 45 °/₀₀ at temperatures of 3–5 and 20–22° C respectively.

At a greater distance (on both sides) of the point of isotonicity the difference becomes smaller. From an external concentration of ca. 31 °/₀₀ onwards both curves follow a nearly parallel course.

2. The point of isotonicity evidently is not a fixed salinity, its position being dependent on temperature. 1) At a temperature of 4° C isotonicity is found in a salinity of ca. 23 °/₀₀, at a tem-

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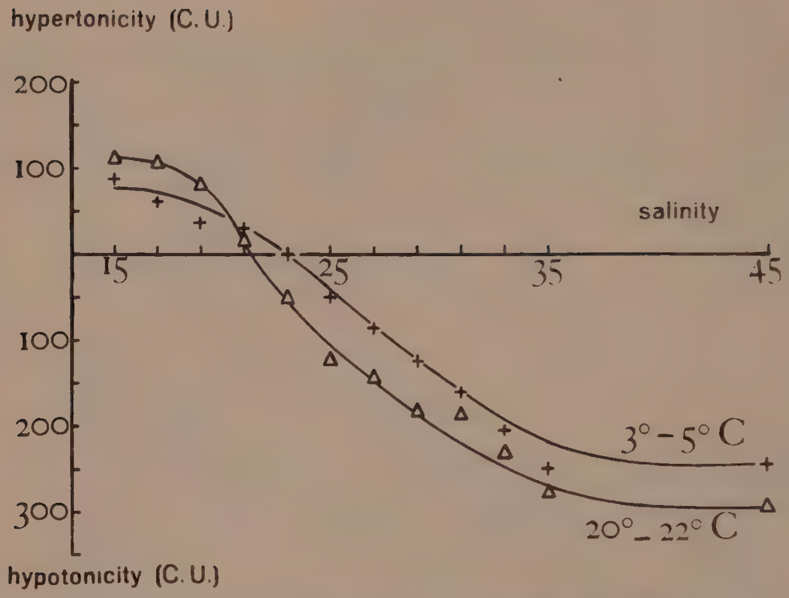
1) By means of an approximating method it could be calculated that the probability of the points of isotonicity being the same at both temperatures amounts to only 1 : 20000.

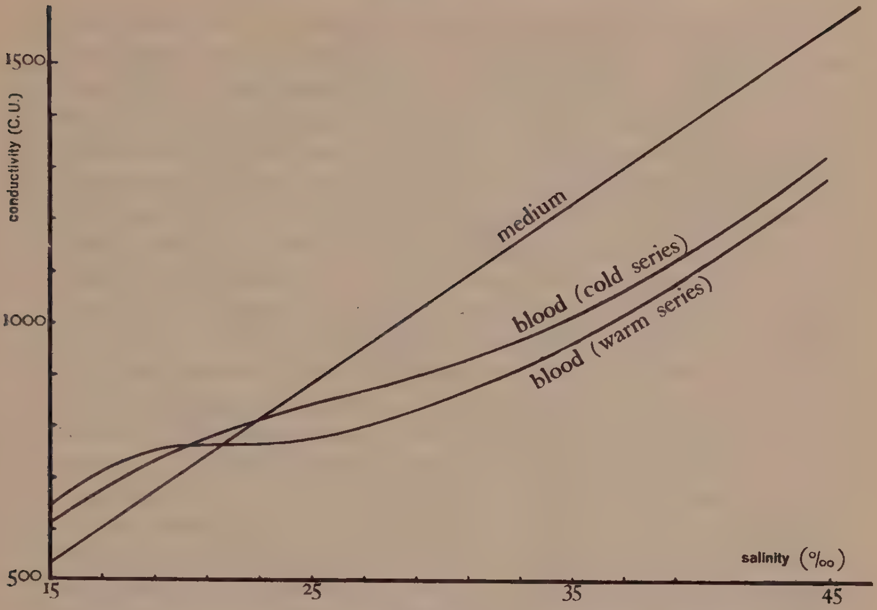


Graph 20*a*. Difference in conductivity between medium and blood in salinities ranging between 15 and 45 $^0/_{00}$ at temperatures of 3–5 and 20–22°C respectively (smoothed curves).

perature of ca. 20° C in a salinity of ca. 21.5 $^0/_{00}$. From the fact that the position of the point of isotonicity depends on temperature it follows that the rule: greater differences between internal and external medium at higher temperatures does not hold for the small range of external salinities between 20.5 and about 21.5 $^0/_{00}$ (see graph 20). This rule would hold without restriction only in case the points of isotonicity should coincide with the point where the concentration of the blood at high and at low temperatures is the same. Graph 20, however, shows that the latter point lies outside the points of isotonicity, at 20.5 $^0/_{00}$ external concentration.

Before making an attempt to co-ordinate these results with those obtained in part I a short summary of the questions arising from part I of this paper may follow here:

1. Why does the salinity optimum shift in a downward direction with increasing temperature? Or, to mention a concrete example: why is it that for full-grown shrimps at a tem-



Graph 20*b* = graph 20 corrected with the aid of the smoothed curves of graph 20*a*.

perature of 20–22° C the salinity optimum is 28–29 $^0/_{00}$, at a temperature of 4° C, however, no less than 33 $^0/_{00}$?

2. Why is it that an extremely low salinity can relatively be better endured at a high temperature, whereas a high salinity is better endured when temperature is low?

The expectation that the knowledge of the osmotic behaviour at different temperatures could give an answer to these questions is realized in so far that it could be proved that the blood concentration, like the position of the salinity optimum, is influenced by temperature. In my opinion we are justified to assume that both facts stand in causal relation to each other, in other words, that the influence exerted by temperature on the position of the salinity optimum is connected with the influence of temperature on the internal concentration. From this it would follow that the internal concentrations corresponding to the optimum external concentrations must be regarded as optimum internal concentrations.

Returning to the blood concentration curves and studying them in connection with this point (question 1 above) we find that the internal concentrations corresponding to the optimum external concentrations at 4° and 22° C amount to 960 and 845 C.U. respectively (according to the corrected graph: 970 and 835 C.U.). These internal concentrations, which we assumed to be the optimum internal concentrations at the given temperatures, appear to be fairly different values. Looking for some point of agreement between these two concentrations it appears, however, that both differ by about the same amount from the corresponding external concentrations. At a temperature of 4° C this difference (= the degree of hypotonicity) amounts to 210 C.U., at a temperature of 20–22° C to 180 C.U. According to the corrected graph the difference amounts to 190 C.U. in both cases. Apparently, therefore, we must suppose that a degree of hypotonicity of ca. 190 C.U. is of some benefit or other to the animal, although the nature of this benefit does not seem clear at the moment. It is further of interest that the interrelation existing between temperature and the salinity optima also holds for temperature and the points of isotonicity. Possibly the two phenomena arise from the same cause, whatever this cause may be.

Question no. 2 leads us to consider the influence of temperature in media of extremely high and extremely low salinity. Graph 20 makes it clear that, generally speaking, the internal concentration goes up and down with the concentration of the external medium. However, except for the points of isotonicity, a certain difference between them is always maintained. Accordingly, continued dilution (concentration) of the external medium will bring about continued dilution (concentration) of the internal medium. We can reasonably assume that continued dilution, resp. concentration of the blood can only be endured within certain limits. Considering that the difference between in- and external medium is always smaller at low than at high temperatures it follows that in the case of continued dilution (concentration) of the external medium the lower (higher) admissible concentration limit for the blood will be exceeded sooner when temperature is low than when it is high.

Assuming this to be correct there must be an extremely high and an extremely low range of salinities which can be endured better at a high than at a low temperature. Or, in other words: although a low temperature is far more favourable generally, the salinity range in which life is possible for the shrimp would have a greater extension (on both sides) at a high temperature. When examining in how far these assumptions are supported by distributional data and by the death rate experiments we come to the following:

1. In extremely low salinities (15 ‰ and less) shrimps can only be found during summer; in a salinity of 35 ‰ (the highest salinity to be found in the North Sea) shrimps occur mainly during winter.

2. In death rate experiments a salinity of 15 ‰ was relatively well endured at a high temperature. At a low temperature a salinity of 15 ‰ proved to be the least favourable of all salinities examined.

3. In the same experiments a salinity of 45 ‰ was extremely unfavourable at a high temperature. At a low temperature this salinity was endured relatively well.

4. During experiments in which blood concentrations were determined in animals kept in a low salinity at a low temperature the animals always proved to be in a strikingly bad condition, most of them being weak and very inactive, seldom taking any food. On the other hand, animals kept in the same salinity at a high temperature made a much better impression. They reacted vigorously on being touched, took large quantities of food, etc. The same applies to animals kept at a *low* temperature in salinities of 25 ‰ and higher.

From these observations those mentioned under 1, 2 and 4 indicate that in all probability the admissible lower limit for the internal concentration at a temperature of 3–5° C is approximated in a salinity of 15 ‰. There is, however, no indication at all that at a temperature of 20° C this limit is reached in the same salinity. As to the extremely high degrees of salinity we see that a salinity of 45 ‰ is reasonably well endured at a low temperature, while at a high temperature this salinity causes death within a few days.

This fact appears to contradict the above mentioned assumption that the blood, because of its being more concentrated at a low temperature than at a high one, would be nearer the admissible upper limit of life at a low temperature. This difficulty would be removed if it could be proved that the upper salinity limit in which life is possible was not reached in my experiments. As long as the blood concentration is not so high as to make life impossible a lower temperature will always be more favourable than a high one, because of its more favourable influence generally. However, by steadily increasing the external concentration a point must be reached where at a low temperature the upper admissible limit for the blood concentration is exceeded. From this point onwards the duration of life will be longer at a high than at a low temperature, until at the high temperature, too, the limit is exceeded.

The assumption that the upper limit of life would lie somewhat higher at a high temperature thus could only be proved by experimenting with shrimps in very high salinities (higher than 45 $^0/_{00}$). Such experiments were carried out in the following way:

Two aquaria, each containing 8 shrimps in about 5 litres of 35 $^0/_{00}$ seawater, were gradually brought to temperatures of 4 and 20° C respectively. After being kept under these conditions for 3 days the animals in both aquaria were subjected to a gradual increase in concentration brought about by the addition of ca. 5 litres of 80 $^0/_{00}$ seawater at a rate of 1 drop/second. Thus, within 2 days the salinity in each of the aquaria was made to increase to ca. 55 $^0/_{00}$.

The protocols dealing with the behaviour of the animals in both aquaria are given below in an unabridged form:

5*th day after the beginning of the experiment:* one animal has died in the cold aquarium. Salinity in both aquaria 49 $^0/_{00}$.

6*th day:* 9 a.m. 2 dead animals in the "warm" aquarium, none in the "cold" one. The "warm" animals still succeed in digging themselves in; on being touched they react with a vigorous flexion of the abdomen.

The "cold" animals do not show these reactions; when put on their back they hardly succeed in struggling to their feet.

4 p.m. "cold" animals in a very bad condition; only very weak movements of the legs were observed. The "warm" animals still succeed in digging themselves in.

8 p.m. 2 of the "cold" animals have died, the rest appears to be in a very bad condition. "Warm" animals still react with flexion of the abdomen on being touched.

11 p.m. "Warm": 5 of the animals have dug themselves in; no 6 is nearly dead. "Cold": the surviving 3 animals are in a very bad condition.

7*th day:* 9 a.m. "Warm": 3 animals have died, the remaining

3 are partly dug in; they move about the aquarium after being touched. "Cold": all animals have died.

10 p.m. The 3 "warm" animals are still alive, 2 of them still reacting with flexion of the abdomen after being touched.

8*th day:* 2 "warm" animals still alive. On being touched they only react with movements of the legs.

10*th day:* the last one of the "warm" animals dies.

The salinities at the end of the experiment were 53·4 $^0/_{00}$ (20° C aquarium) and 52·9 $^0/_{00}$ (4° C aquarium).

The experiment was repeated with approximately the same result. In this case the difference between "warm" and "cold" animals was somewhat less conspicuous than in the first experiment.

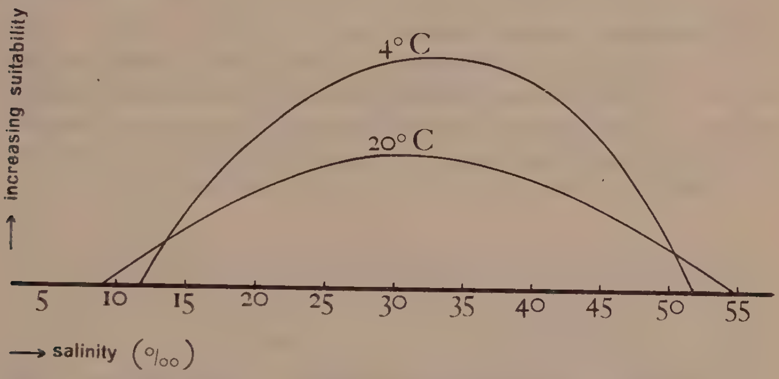


Fig. 6. Schematic representation concerning the suitability of media of various salinities at high and low temperatures.

Both experiments lead to the conclusion that extremely high salinities are slightly better endured when the temperature is high than when it is low, notwithstanding the fact that high temperatures are very unfavourable generally. That the animals all died within a very short period of time need not cause any surprise; the admissible upper limit for the internal concentration was probably exceeded in the "warm" as well as in the "cold" animals. However, death rates and notably the difference in condition between the animals kept at high and at low temperatures suggest that this limit was exceeded sooner (i.e. at a lower salinity) at a low than at a high temperature, though it must be admitted that the differences observed are rather small. Of course, it must be borne in mind that the salinities used in these experiments are quite outside the "natural" range of salinities. In fact, the experiments were only carried out from theoretical considerations.

Fig. 6 gives a schematic representation of the conclusions reached thus far. These conclusions may be summarized as follows:

1. Generally, a low temperature is more favourable than a high one.
2. The salinity range in which the shrimp is able to live has a greater extension (on both sides) at a high than at a low temperature.
3. At a high temperature the salinity optimum is lower than at a low one.

The diagram further illustrates that a salinity of 45 ⁰/₀₀ can be better endured at a low than at a high temperature, but that on still further increasing the concentration of the external medium the higher temperature becomes the more favourable. The same takes place when the external medium is more and more diluted.

IV. Influence of temperature on the adaptation to changed external concentrations.

The experiments described in part I showed that a relatively great number of animals die within the first one or two days after being transferred into a medium of higher or lower concentration. Especially at a high temperature mortality during acclimatisation is exceptionally high. It therefore seemed of interest to investigate the course of adaptation of the blood to changed external concentrations at various temperatures. The process of adaptation to increased as well as to decreased external concentrations was studied, special attention being paid to the first 10 hours after transfer of the animals.

1. The effect of a decrease in external concentration from 32.3 to 15.3 ⁰/₀₀ was examined at temperatures of 4, 16 and 21° C.
2. The effect of an increase in external concentration from 32.3 to 44.7 ⁰/₀₀ was examined at temperatures of 4, 16 and 21° C.

3. The effect of a decrease in external concentration from 32.3 to 25 $^{0}/_{00}$ was examined at temperatures of 4 and 21° C.

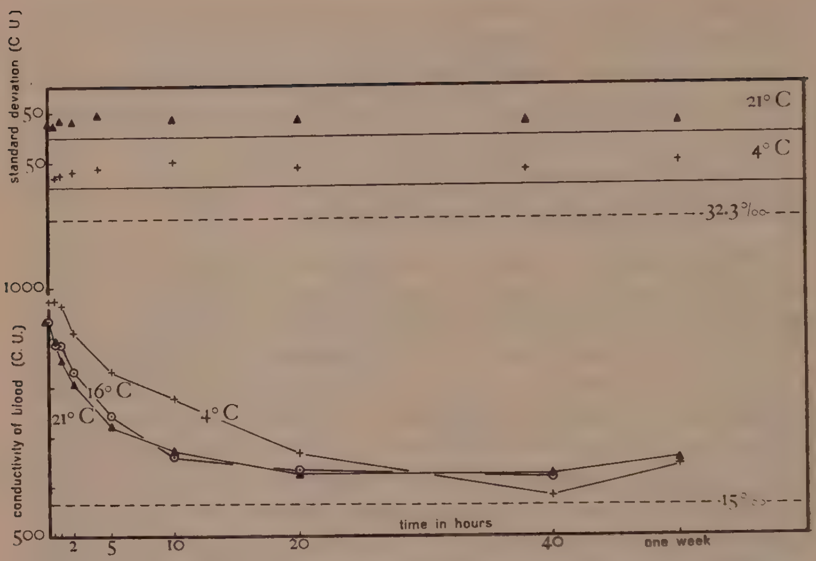
4. The effect of an increase in external concentration from 30 to 35 $^{0}/_{00}$ was examined at temperatures of 4 and 21° C.

1. *External concentration lowered from* 32.3 *to* 15.3 $^{0}/_{00}$ *at temperatures of* 4, 16 *and* 21° C. See graph 21.

A great number of animals were kept for at least a week in one of the aquarium tanks of the station, the salinity of which was about 30 $^{0}/_{00}$, whereas the temperature was about 15° C. After that, they were transferred to a number of small aquaria, containing seawater of 32.3 $^{0}/_{00}$. Temperature was gradually brought to the desired degree in the course of about two days. The animals were left under these conditions for at least 4 days. Thereupon, the conductivity value for the blood was determined in at least 10 animals. The remaining animals were transferred (without intermediate stages) to a salinity of 15.3 $^{0}/_{00}$, temperature remaining the same. Groups of 10 animals each were examined ½, 1, 2, 5, 10, 20 and 40 hours after the transfer took place. The concentration of the external medium was continually checked by conductivity determinations and Cl titrations. The results are represented in graph 21.

In a salinity of 32.3 $^{0}/_{00}$ the animals are hypotonic in regard to their medium, the degree of hypotonicity being greater at a high than at a low temperature. Consequently, in a salinity of 32.3 $^{0}/_{00}$ the lowest blood concentration is recorded at the highest temperature. On the other hand, in a salinity of 15.3 $^{0}/_{00}$, in which the blood is hypertonic, the lowest blood concentration is recorded at the *lowest* temperature. The curves representing the course of adaptation at high and at low temperatures accordingly intersect at a given moment (see graph 21). The rate of adaptation appears to be much higher at a high than at a low temperature. The difference between the 16 and 21° C adaptation curves is rather small; only during the first 5 hours do the 21° C animals show a higher rate of adaptation.

It further appears that during adaptation the average blood concentration reaches a minimum value, which, especially at a low temperature, is far below the ultimate one. At a temperature of 21° C this minimum value is reached after about 20,



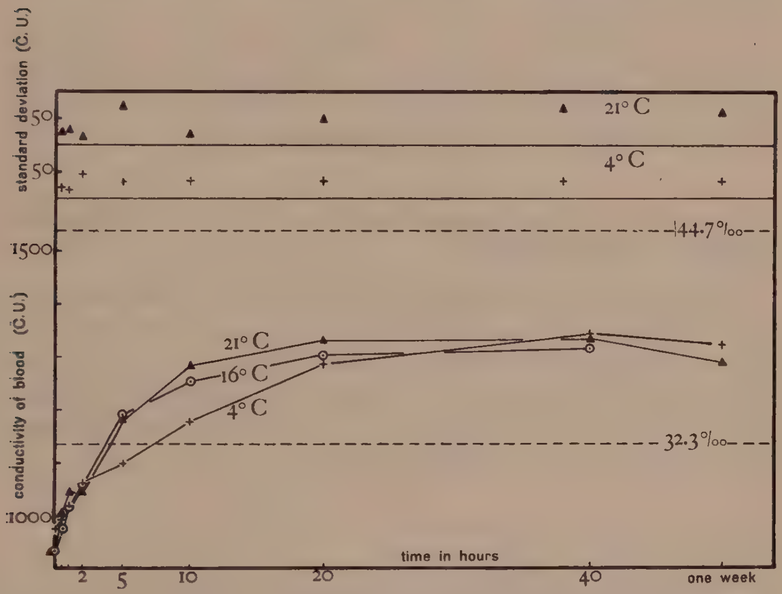
Graph 21. Adaptation to decreased salinity (32.3 to $15.3\,^0/_{00}$) at temperatures of 4, 16 and 21° C.

at 4° C after about 40 hours. It is possible, however, that the latter value is abnormally low in consequence of the extremely bad condition of the animals. A prolonged presence in the $15\,^0/_{00}$–4° C medium probably would have caused most of the animals to die within a week.

The average conductivity value for the animals kept for a week in a medium of $15\,^0/_{00}$–4° C, which is added to the graph, cannot altogether be compared with the value "after 40 hours". This additional point represents the average for a number of animals which were gradually acclimatized to the low external salinity; hence their condition was considerably better than that of the "40 hour" animals. Nevertheless, the very low internal concentration of the "40 hour" animals at 4° C points to the osmoregulation being checked some way or other by the low temperature. At a temperature of 4° C the blood becomes ever more diluted, while at a temperature of 21° C the dilution is brought to a standstill 20 hours after the transfer took place. During the next 20 hours the blood even increases in concentration.

2. *Increase in external concentration from* 32.3 *to* 44.7 $^0/_{00}$ *at temperatures of* 4, 16, *and* 21° C. See graph 22.

Both in a medium of 32.3 and in a medium of 44.7 $^0/_{00}$ the animals are hypotonic. The degree of hypotonicity is greater at a high than at a low temperature. The 16 and 21° C curves show minor differences only. The rate of adaptation is highest at a temperature of 21° C. Accordingly, during the time elapsing between 2 and ca. 30 hours after transfer the blood concentration is highest at this temperature.



Graph 22. Adaptation to increased salinity (32.3 to 44.7 $^0/_{00}$) at temperatures of 4, 16 and 21° C.

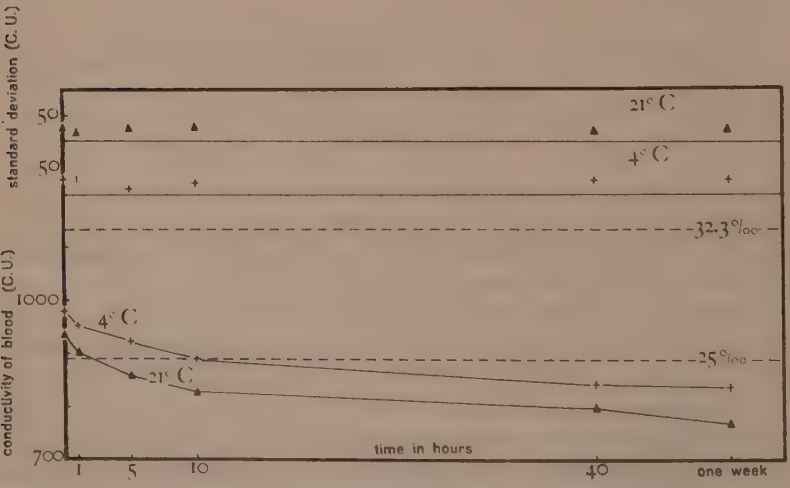
The average conductivity values for animals kept for a week in a medium of 44.7 $^0/_{00}$ appear to be lower than those reached after 40 hours. Probably here, too, a maximum blood concentration is reached during adaptation. It might also be possible, however, that selection plays a part in this case, and that during the time elapsing between 40 hours and one week after the transfer those animals that reached the highest blood concentration died. This supposition, however, is practically ruled out by the fact that the range of individual values is about the same for the "40 hour" and for the "one week" animals. The latter range even includes higher internal concentrations than those found in the "40 hour" animals.

3. *Lowering of the external concentration from* 32.3 *to* 25 °/₀₀ *at temperatures of* 4 *and* 21° C. See graph 23.

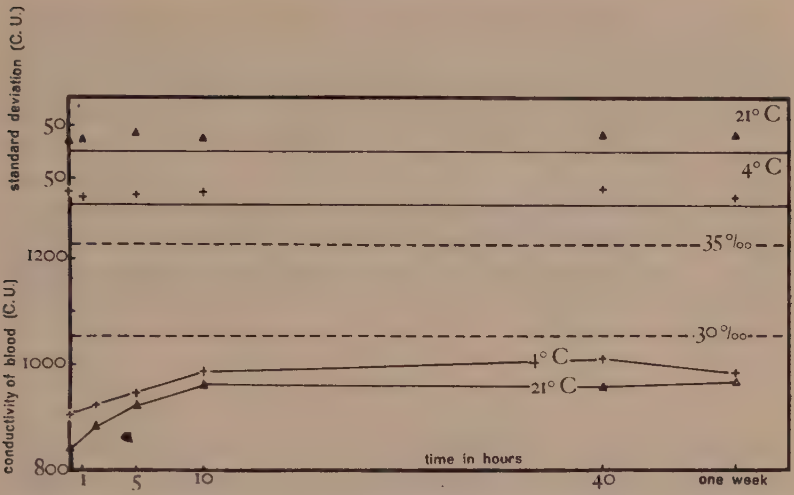
Both in a salinity of 32.3 °/₀₀ and in a salinity of 25 °/₀₀ the animals are hypotonic. The degree of hypotonicity is greater at 21 than at 4° C. At a temperature of 21° C the rate of adaptation is somewhat greater than at a temperature of 4° C.

4. *Increase of external concentration from* 30 *to* 35 °/₀₀ *at temperatures of* 4 *and* 21° *C*. See graph 24.

In this case, too, the animals are hypotonic in both media, the degree of hypotonicity being greatest at a temperature of 21° C. The rate of adaptation is greater at 21 than at 4° C. At a temperature of 4° C the blood concentration attains a maximum 40 hours after transfer of the animals. During the following hours the average conductivity value decreases.



Graph 23. Adaptation to decreased salinity (32.3 to 25 °/₀₀) at temperatures of 4 and 21° C.



Graph 24. Adaptation to increased salinity (30 to 35 $^0/_{00}$) at temperatures of 4 and 21° C.

Summarizing the results of the adaptation experiments we come to the following.

1. The rate of adaptation always is greater at high than at low temperatures.

2. During adaptation to increased as well as decreased external concentrations the average blood concentration may reach a value higher resp. lower than the ultimate one. This is especially striking at a low temperature.

3. During the first 5 hours after a change in concentration the rate of adaptation is relatively high, especially at a high temperature. Probably this rapid initial change in internal concentration makes great demands upon the animals; hence the high initial mortality in the 20–22° C death rate experiments.

V. Influence of changed temperature on the internal concentration, the external concentration remaining the same.

The experiments mentioned under III demonstrate that shrimps kept at different temperatures in media of a given concentration have a different internal concentration. The series of experiments to be described below were carried out with the object of determining the rate at which change of the internal concentration takes place when temperature is changed. The salinity of the external medium was kept as constant as possible.

Since rapid and considerable changes in temperature can hardly be endured by the animals I made use of temperature changes not exceeding 10° C. The transitions were made in such a way as to correspond as much as possible to temperature-salinity conditions occurring in nature. However, in order to obtain more distinct effects, greater and more sudden changes in temperature were applied than those taking place under natural circumstances.

Series 1

Shrimps kept in a salinity of ca. $15\,^0/_{00}$ were subjected to a decrease in temperature from ca. 15 to ca. 5° C. This experiment forms an exaggerated imitation of the natural situation taking place during autumn.

Fifty animals were kept during 4 days in a salinity of $15\,^0/_{00}$ at a temperature of 14–16° C. After that, the average blood concentration was determined in 10 animals. Next, the aquaria containing the other 40 animals were placed in water of 4° C, causing the temperature in the aquaria to decrease to ca. 5° C in the course of 2½–3 hours. The average conductivity value for the blood was determined 2, 4½, 21½ and 42 hours after the transfer of the aquaria. The results are given in table 16.

TABLE 16

Average conductivity of blood during and after a 10° C decrease in temperature, in a constant salinity of ca. $15\,^0/_{00}$

time in hours after temperature had begun to decrease	temp. in ° C	salinity of medium in $^0/_{00}$	conduct. of medium in C.U.	average conduct. of blood in C.U.	standard deviation $\left(\sqrt{\frac{\Sigma V^2}{n-1}}\right)$ in C.U.	number of animals
	15	15.4	556	674	28	9
2	5.5	15.4	555	680	28	9
4.5	4.2	15.4	546	686	30	10
21.5	3.2	15.5	555	637	25	10
42	5	15.5	555	651	24	10

During the first 4 hours no appreciable change in blood concentration occurs; after a period of 21.5 hours the average blood concentration has diminished by ca. 4%. During the following 20 hours a slight increase in blood concentration takes place, possibly in connection with an increase in temperature from 3.2 to 5° C.

On the whole, a decrease in temperature of about 10° C appears to cause a slight fall in blood concentration. In this case this means a slight decrease in hypertonicity, which fits in with the results of previous experiments.

Series 2

Shrimps kept in a salinity of 25 $^{0}/_{00}$ were subjected to a decrease in temperature from 15 to 5° C. This experiment again imitates the natural situation during autumn in an exaggerated way.

The series was carried out in the same way as series 1. The average blood concentration was determined $2\frac{1}{2}$, 10, 20, 42 and 72 hours after transfer of the aquaria to water of 4° C. For results see table 17.

TABLE 17

Average conductivity of blood during and after a 10° C decrease in temperature, in a constant salinity of ca. 25 $^{0}/_{00}$

time in hours after temperature had begun to decrease	temp. in ° C	salinity of medium in $^{0}/_{00}$	conduct. of medium in C.U.	average conduct. of blood in C.U.	standard deviation $\left(\sqrt{\frac{\Sigma V^2}{n-1}}\right)$ in C.U.	number of animals
	15	24.8	885	794	36	10
2.5	5.5	24.7	882	804	25	10
10	4.2	24.9	90[illegible]	816	21	7
20	4.5	24.9	893	825	20	10
42	3.5	24.8	885	832	43	10
72	6		903	828	25	10

In this medium a decrease in temperature brings about an increase in average blood concentration, which means a decrease in hypotonicity. The increase in average blood concentration during the first 10 hours is of no significance, as the external medium also increased in concentration. The increase in blood concentration mainly takes place 10–20 hours after the temperature was changed.

Series 3

Shrimps kept in a salinity of ca. $35\,^0/_{00}$ were subjected to an increase in temperature from 5 to 15° C. The experiment imitates the natural situation taking place during spring in an exaggerated way.

Determinations of the average blood concentration were carried out 2, 5½, 12½, 21½, 42½ and 72 hours after temperature was made to increase. The results are given in table 18.

TABLE 18

Average conductivity of blood during and after a 10° C rise in temperature, in a constant salinity of $35\,^0/_{00}$

time in hours after temperature had begun to increase	temp. in ° C	salinity of medium in $^0/_{00}$	conduct. of medium in C.U.	average conduct. of blood in C.U.	standard deviation $\left(\sqrt{\frac{\Sigma V^2}{n-1}}\right)$ in C.U.	number of animals
	3.5	34.7		1015	24	10
2	13.5	34.8	1236	1011	32	10
5.5	15	35.0	1228	1018	61	9
12.5	15	34.8	1235	974	25	7
21.5	15	34.9	1242	989	37	8
42.5	15	34.9	1230	992	24	9
72	15	35.0	1239	1009	30	9

The results of this series are not clear. In the light of previous experience one would expect the average blood concentration to fall. In reality it remains about the same during the first 5–6 hours, after which a distinct fall sets in. This is followed by a slight, but gradual increase 21, 42 and 72 hours after transfer. The ultimate value does not differ from the initial one. In interpreting the results we have to take into account that in a medium of $35\,^0/_{00}$ a difference of 10° C only has a relatively small influence on the blood concentration. According to previous experiments (see graph 20) average blood concentrations in a salinity of 35 $^0/_{00}$ at temperatures of 4 and 20° C amount to 980 and 960 C.U. respectively. The difference in this case is much smaller than in a salinity of 25 $^0/_{00}$, where the corresponding average conductivity values amount to 835 and 765 C.U. respectively.

VI. Average blood concentration in shrimps kept during spring and autumn under natural temperature conditions and at a constant temperature
a. during spring,
b. in autumn.

The experiments were carried out to make certain:

1. whether the natural environmental changes taking place during spring and autumn bring about a change in blood concentration;

2. whether this latter change is solely due to change in temperature, since one might also assume a periodicity caused by other influences, e.g. an autonomous periodicity or a periodicity caused by light.

In the later part of autumn (resp. spring) a number of shrimps were distributed over two large basins, both containing seawater of a salinity of about 30 $^0/_{00}$. One of these basins was placed in an unheated room, where temperature was allowed to increase and decrease with the outside temperature. Water from the seawater duct of the station was injected into the basin so that no special aeration had to be used. The other basin was kept at a constant temperature, identical with the temperature in the unheated room at the beginning of the experiment. Since no flowing water could be used here the water was changed every 2–3 weeks, care being taken to avoid any changes in temperature. The water was continually aerated. Stress must therefore be laid on the fact that both media were not strictly comparable, but it is assumed that this has been of no influence on the course of the experiments.

Both basins were placed in full daylight in order that they might be exposed to the seasonal changes in light intensity. The average blood concentration was determined at regular intervals in 4 animals from both basins.

Owing to technical difficulties the experiments gave rather bad results and they are therefore given for what they are worth.

a. Spring experiment

The experiment lasted from May the 5th until August the 3rd, 1939. During this period temperature in one basin rose from 11 to 18° C, while in the other basin the temperature was constantly kept at about 10° C.

The salinity in the basin where temperature was allowed to rise varied between ca. 29 and 32 $^0/_{00}$. The salinity in the other (cooled) basin showed a tendency to decrease as a result of condensation of water from the air. Generally the salinity amounted to about 30 $^0/_{00}$. For technical reasons it was impossible to keep the salinity in both basins at exactly the same level, hence the average blood concentrations in both groups of animals can not directly be compared. For this reason the difference in conductivity value between in- and external medium is recorded for each separate case (see table 19).

The number of determinations (4), from which the average values were calculated, is undoubtedly too small for reliable figures. Accordingly, the results, when considered one by one, are rather irregular.

Generally, at a constant temperature of 10° C, the difference in conductivity between in- and external medium neither increases nor decreases. Comparing, for instance, the first 5 values given in column 5 with the last 5 it appears that the averages over both periods show no great difference: 170 and 157 C.U. respectively, while the average conductivity values for the external medium during the same periods are 1060 and 1056 C.U.

In the basin where temperature gradually rose from 13 to 18.2° C the difference between internal and external concentration (column 10) generally shows a slight tendency to increase. The average of the first 5 differences amounts to 177 C.U., while the remaining 5 differences give an average of 210 C.U. However, this increase can only partly be ascribed to the influence of increasing temperature: comparing the average concentration of the external medium over both periods we see that during the second period the concentration was considerably higher than during the first one: 1100 against 1055.

From graph 20 we see that at a temperature of 20° C the difference between internal and external medium amounts to 175 in an external medium of 1055 C.U., and to 185 in an ex-

TABLE 19

Average conductivity of blood during May–August 1939 under natural and constant temperature conditions

constant temperature

date 1.	temp. in °C 2.	average conduct. of blood in C.U. 3.	conduct. of medium in C.U. 4.	average difference between blood and medium in C.U. 5.
11-5-'39	10	896	1072	176
24-5	10	927	1101	174
1-6	10	897	1046	149
8-6	10	858	1046	188
13-6	10	870	1033	163
19-6	10.8	910	1048	138
1-7	10.5	895	1060	165
9-7	10.0	883	1072	189
15-7	10.0	930	1060	130
21-7	10.6	909	1047	138
27-7	10.4	880	1044	164

increasing temperature

date 6.	temp. in °C 7.	average conduct. of blood in C.U. 8.	conduct. of medium in C.U. 9.	average difference between blood and medium in C.U. 10.
15-5	13	872	1035	163
25-5	14.5	871	1063	192
31-5	14.5	885	1045	160
8-6	15.4	873	1063	190
14-6	15.5	886	1068	182
19-6	16.0	892	1121	229
3-7	17	869	1101	232
14-7	17.5	903	1111	208
20-7	18.1	899	1093	194
3-8	18.2	887	1072	185

ternal medium of 1099 C.U. This discrepancy arises from the fact that in this salinity range a certain increase in external concentration results in an increase in internal concentration smaller than that of the external concentration.

When interpreting the results recorded in table 19 this fact must of course be taken into account. The difference between both average values accordingly has to be reduced by 10 C.U., leaving a difference of ca. 23 C.U., which can eventually be attributed to the difference in temperature during the two periods. This difference is by no means great, but considering that the average difference in temperature during the two periods only amounted to 4° C, no great difference could be expected.

Summarizing, we can state that from the beginning of May to the beginning of August no autonomous decrease in blood concentration other than that due to temperature takes place; a slight decrease in blood concentration is found in those animals which are subjected to the natural increase in temperature.

b. Autumn experiment

The experiment lasted from Oct. the 10th until Dec. the 5th, 1939. During this period a number of animals were kept at a constant temperature of 16° C, while another group was subjected to the natural decrease in temperature taking place during this period, from 16 to about 9° C. Fortnightly the average blood concentration, together with the concentration of the external medium, was determined in 10 animals out of each group. The results are represented in table 20, which also gives the difference between in- and external concentration for each group of determinations.

In the animals kept at a constant temperature of 16° C the difference in concentration between in- and external medium remains about the same during the whole period. The differences found on 25-10-'39 and 10-11-'39 are considerably greater than those found on 13-10-'39 and 24-11-'39; this is probably caused, at least in part, by the greater concentration of the external medium during this part of the experiment (see also graph 20).

Animals subjected to a steadily decreasing temperature show an increase in average blood concentration. This becomes particularly clear when we compare the first and the last differences

TABLE 20

Average conductivity of blood during Oct.-Dec. 1939 under natural and constant temperature conditions

constant temperature

date	temp. in °C	average conduct. of blood in C.U.	conduct. of medium in C.U.	salinity of medium in $^0/_{00}$	average difference between blood and medium in C.U.
13-10’39	16.5	891	1060	29.8	169
25-10-’39	15.1	962	1155	31.3	193
10-11-’39	16.0	878	1185	31.1	207
24-11-’39	14.5	907	1073	30.6	166

decreasing temperature

date	temp. in °C	average conduct. of blood in C.U.	conduct. of medium in C.U.	salinity of medium in $^0/_{00}$	average difference between blood and medium in C.U.
10-10-’39	13	848	1029	29.2	181
24-10-’39	12	865	1020	29.1	155
7-11-’39	10	879	1044	29.3	165
21-11-’39	10	891	1044	29.5	153
5-12-’39	8	885	1030	29.1	145

between in- and external concentration. The external concentration was about the same in both cases, the difference decreased from 181 to 145 C.U. Summarizing, we can say that during autumn no autonomous change in blood concentration takes place. An increasing blood concentration was recorded in animals subjected to the natural decrease in temperature taking place between early October and the beginning of December.

VII. Comparison of average blood concentration in:
a. younger and older specimens;
b. ovigerous and non-ovigerous females.

The different behaviour as to distribution and migration of younger and older specimens, of ovigerous and non-ovigerous females was the immediate motive for the experiments to be described in the following. If a connection exists between migration and temperature and salinity on the one, and between the blood concentration and these milieu factors on the other hand it seemed probable that the blood concentration would be different in groups which show a different behaviour in respect to distribution and migration.

a. Younger and older specimens

In the first place attention is drawn to groups of different ages.

Both HAVINGA's distributional data and the result of the death rate experiment described on page 21 indicate that younger animals are able to endure a low salinity much better than the older specimens. I therefore expected that younger animals would be able to maintain a greater difference between in- and external medium, especially in low external concentrations. Another possibility would be that in the younger animals the lower admissible limit for the blood concentration would be lower than in older animals.

Average blood concentrations were determined in 24 "young" animals (age about 16 months, length from rostrum to tail 4–5 cm) and 10 "old" animals (age about 2 years and 9 months, length from rostrum to tail 6.9–7.3 cm). Before the determinations were carried out the animals were kept four days in a salinity of 25.3 $^0/_{00}$ at a temperature of about 20° C.

Provided that a dilution of about 300 times is used the amount of blood which can be taken from a young animal is sufficient for one determination. No duplicate determinations could therefore be made, so that the results are less reliable than those obtained with full-grown shrimps. As a result of the greater dilution the figures will generally be rather high (see graph 19).

For the 24 young animals an average conductivity value of 703 C.U. was found (maximum 769, minimum 633). The average conductivity value for the old animals amounted to

ERRATA

Page 88, 10th line from below, salinity of 25·3 % should be: salinity of 15·3 %.

Page 89, 10th line from above, amounted to 894 and 890 respectively should be: amounted to 694 and 690 respectively.

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701 C.U.[1]) (max. 732, min. 663). The conductivity value for the external medium amounted to 562 C.U. in both cases. Consequently, no difference in average blood concentration between the two age groups could be proved.

Neither could a difference in blood concentration between young and old animals be found in a salinity of 19.3 °/₀₀ (temp. 20° C). Conductivity values in this case amounted to 776 C.U. for 19 young animals (max. 849, min. 720) and to 778 C.U. for 17 old animals (max. 833, min. 727). Conductivity values for the external medium amounted to 894 and 890 C.U. respectively.

Finally, I determined average blood concentrations in animals kept in a salinity of 34.7 °/₀₀ at a temperature of 4–5° C. Here, too, no difference could be proved to exist between young and old animals, the average value for 18 young animals being 1006 (max. 1058, min. 957), for 10 old animals 1015 C.U. (max. 1052, min. 969).

The above figures show that young shrimps do not maintain a greater difference between in- and external medium than the older ones. In connection with distributional data it may therefore be assumed that they can bear a very low internal concentration better than the older specimens.

It is also possible that in shrimps younger than 16 months the internal concentration differs from that of the older ones. In these very young specimens the amount of blood is extremely small, however, so that no reliable data could be obtained.

b. Ovigerous and non-ovigerous females

According to HAVINGA (1930) egg-bearing females generally can only be found in the more saline part of the total area of distribution.

As stated in Part I a similar behaviour is found, among other species, in *Eriocheir sinensis*. Now, SCHOLLES (1930) states that egg-bearing females of this species, when transferred into fresh water, do not succeed in keeping up a normal blood concentration; they even die within 2–5 days. Outside the spawning season *Eriocheir* is perfectly able to live in fresh water.

In egg-bearing females of *Crangon* mortality in media of a low salinity is not exceptionally high. Nevertheless, it seemed worth while to investigate whether in this species the egg-bearing females are able to maintain a normal blood concentration when kept in a medium of low salinity. To this end a number of determinations were carried out with animals kept in salinities of 17, 19, 21 and 23 $^0/_{00}$ at a temperature of 20° C.

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[1]) In comparison with previous results the conductivity values both for young and for old animals are exceptionally high. The reason for this deviation is unknown.

The difference in blood concentration between ovigerous and non-ovigerous females proved to be insignificant, however. The average blood concentrations of egg-bearing females were 733, 793, 789 and 805 C.U. respectively; corresponding values for females without eggs were: 739, 770, 800 and 806 C.U.

In the experiments described under I–VII a small number of the animals involved were egg-bearing females. In these cases, too, no systematic deviation of the blood concentration was observed.

It should be added that the limited range of distribution of egg-bearing females may also be caused by the fact that parent animals lose their eggs when penetrating into low salinities (see Part I, sub III).

VIII. Weight determinations during adaptation to decreased or increased external concentration.

Contrary to expectation I generally found that animals kept in a low salinity contained less blood than those kept in a higher salinity.

Animals kept for some time in a salinity of 15 $^0/_{00}$ generally only yielded $\frac{1}{2}$–$^2/_3$ of the amount of blood which could be collected from animals kept in a salinity of 20 $^0/_{00}$ and higher.

As a matter of fact this statement is rather subjective. The amount of blood which can be collected from one animal greatly depends upon the way in which certain details of the collecting method (see page 60) are carried out. However, in the course of this investigation, in which the collecting of blood was a daily routine, these manipulations became more and more uniform and effective, so that at last a maximum quantity of blood could be collected from each individual. Under these circumstances at least some value may be attached to the otherwise personal impression. As this impression is exactly the opposite of what could be expected a priori I tried to gain more objective data by weighing the animals at regular intervals during adaptation to a changed external concentration.

However, this procedure, too, proved to have a serious drawback. In order to remove the adhering seawater the animals had to be wrapped up in a dry towel for one or two minutes before being weighed, and most animals which were "dried" more than once during 24 hours died within a few days. Thus, it is doubtful whether the animals, all being in a more or less bad condition during the experiments, behave normally as to their osmoregulation. Nevertheless, some of the results are given here. Each weighing is accurate to about 10 mg, that is to say, in successive weighings of one individual, replaced in seawater after each weighing, the results showed differences of 10 mg at most.

a. Weight of animals transferred from a salinity of 25 $^0/_{00}$ to a salinity of 15 $^0/_{00}$ at a temperature of 19° C. See table 21.

b. Weight of animals transferred from a salinity of 25 $^0/_{00}$ to a salinity of 15 $^0/_{00}$ at a temperature of 15° C. See table 22.

c. Weight of animals transferred from a salinity of 25 $^0/_{00}$ to a salinity of 35 $^0/_{00}$ at a temperature of 15° C. See table 23.

The figures given in the tables 21, 22 and 23 indicate that neither transfer to higher salinities nor transfer to

TABLE 21

Weight during acclimatisation to a decreased salinity (25 $^0/_{00}$ to 15 $^0/_{00}$, temperature 19° C)

animal	weight in 25 $^0/_{00}$ (gr)	weight, 5 hours after transfer into 15 $^0/_{00}$ (gr)	10 hours (gr)	24 hours (gr)	35 hours (gr)	48 hours (gr)
1	8.90	8.90	8.90	8.86	8.86	†
3	8.64	8.72	8.71	8.69	8.67	8.67
5	8.34	8.40	8.39	8.36	8.36	†
7	8.63	8.66	8.69	8.68	8.65	†
2	8.80			8.78		†
5*a*	8.69			8.69		8.73
6	8.42			8.42		8.42
8	8.25			8.29		8.28

TABLE 22

Weight during acclimatisation to a decreased salinity (25 ⁰/₀₀ to 15 ⁰/₀₀, temperature 15° C)

animal	weight in 25 ⁰/₀₀ (gr)	10 hours after transfer in 15 ⁰/₀₀ (gr)	24 hours (gr)	48 hours (gr)
2	8.11	8.12	8.01	8.20
3	8.36	8.36	8.33	8.38
4	7.95	8.00	7.99	7.97
7	7.85	7.86	7.88	7.81
8	8.90	8.97	8.98	8.88

TABLE 23

Weight during acclimatisation to an increased salinity (25 ⁰/₀₀ to 35 ⁰/₀₀, temperature 15° C)

animal	weight in 25 ⁰/₀₀ (gr)	10 hours after transfer in 35 ⁰/₀₀ (gr)	24 hours (gr)	48 hours (gr)
2	8.24	8.24	8.25	8.19
3	8.79	8.80	8.83	8.83
4	8.07	8.11	8.09	8.08
5	8.32	8.33	8.34	8.39
8	8.66	8.55	8.48	8.25
9	8.36	8.33	8.33	†

lower salinities involves an outspoken change in weight. Thus, during adaptation no osmotic intake or loss of water great enough to be measured seems to take place, not even in animals which obviously are in a bad condition. It therefore appears that the decreased quantity of blood I obtained from animals kept at a low salinity is not accompanied by a decrease in weight.

IX. Blood concentration shortly after moulting.

Animal no 8 (see table 23) forms an exception to the rule that during adaptation to an increased external concentration no change in body weight takes place. This animal, which moulted very shortly before being transferred to a medium of higher salinity, systematically decreased in weight. This indicates that in a normal case the exoskeleton forms a considerable obstacle to the exchange between the in- and external medium.

That the loss in weight recorded in the newly moulted animal should accompany each case of moulting seems improbable; observations on other Crustacea (BAUMBERGER and OLMSTED 1928) make it clear that usually water is absorbed shortly after moulting. That the exchange between blood and medium greatly increases during or shortly after moulting further appears from a number of conductivity determinations with newly moulted animals. In these animals the difference in concentration between in- and external medium always proved to be considerably smaller than in "normal" cases. This applies to animals which are hypotonic as well as to those which are hypertonic in respect to their medium. Table 24 may serve to make this clear. It was compiled from a number of determinations belonging to experiments already described (adaptation experiments, etc.). When in one of these experiments one or more of the animals happened to have moulted shortly before, the blood concentration was

TABLE 24

Conductivity of blood shortly after moulting, in media of various salinities

conduct. medium in C.U.	average conduct. of 8–9 „hard" animals in C.U.	difference in conduct. between medium and blood („hard" animals) in C.U.	conduct. of blood of a newly moulted animal in C.U.	difference in conduct. between medium and blood („soft" animals) in C.U.
540	685	45	564	24
568	808	240	665	97
694	776	82	656	38
1096	911	185	993	103
1205	882	323	971	234
1205			907	298
1235	974	261	1065	170
1538	1020	518	1126	412
1538			1163	365

determined all the same, although the result was left out of account in the calculation of average concentrations.

Summary of part II

1. *Crangon* is homoiosmotic. [1] The blood concentration, however, is not independent of the concentration of the external medium; an increase (decrease) in external concentration results in an increase (decrease) in internal concentration, although in general to a much smaller degree.

2. In salinities lower than 21–23 $^0/_{00}$ *Crangon* is hypertonic, in those higher than 21–23 $^0/_{00}$ *Crangon* is hypotonic in respect to its medium.

3. The difference between in- and external concentration is greater at high than at low temperatures; this applies both to those situations where the animal is hypotonic and to those situations where the animal is hypertonic in respect to its medium.

4. The position of the point of isotonicity partly depends on temperature: at a temperature of 20° C isotonicity prevails in a salinity of about 21.5 $^0/_{00}$, at 4° C in a salinity of about 23 $^0/_{00}$.

5. Shrimps which were subjected to the seasonal increase (decrease) in temperature taking place during spring (autumn) showed a slight decrease (increase) in internal concentration. That this decrease (increase) is directly related to the change in temperature, no other seasonal influence being involved, could be proved by comparing the influence of a changing with that of a constant temperature. In the animals kept at a constant temperature no seasonal decrease or increase in blood concentration could be recorded.

6. Adaptation of the internal concentration to a change in external concentration takes place at a higher rate as temperature is higher. During adaptation to a medium of *much* higher (lower) concentration the blood concentration reaches a maximum (minimum) value which may considerably exceed the final blood concentration in the new medium. These

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[1] The term „homoiosmotic'' is used here in the broader sense suggested by KROGH (1939, p. 8).

maxima (minima) are more outspoken when temperature is low than when it is high, indicating that osmoregulation is more or less checked by low temperatures.

7. In a constant salinity of 15 $^0/_{00}$ a decrease in temperature of 10° C brings about a decrease in blood concentration. In a constant salinity of 25 $^0/_{00}$, on the other hand, the same decrease in temperature brings about an increase in blood concentration. It is important to note that in both cases the difference between in- and external concentration becomes smaller.

8. Neither during increase nor during decrease in external concentration a change in weight could be recorded.

9. In newly moulted shrimps the difference between in- and external concentration is always smaller than in "hard" animals.

10. No difference in average blood concentration could be proved to exist in young and old animals (aged 16 months and 33 months respectively). As young animals apparently are able to stand much lower salinities than the older specimens it would seem that in the younger animals the lower admissible limit for the blood concentration is lower than for the older animals.

Nor could a difference in blood concentration be recorded in ovigerous and non-ovigerous females. The fact that ovigerous females do not occur in low salinities might possibly be caused by the parent animals losing their eggs in media of low salinity.

GENERAL SURVEY

The original object of this investigation was to try and find an explanation for the distribution of *Crangon crangon* L.

The fact that this distribution shows a marked seasonal change made it conceivable, especially in connection with former experiments (BROEKHUYSEN 1936, CAUDRI 1937), that we should have to do with a combined influence of temperature and salinity.

Briefly, the seasonal change in distribution of *Crangon* comes to the following. During winter the animals can be found in the coastal regions of the North Sea and in a small part of the adjoining shallows; that is to say, in an area of relatively high salinity. During spring a general migration takes place towards the brackish waters, where the animals remain in great numbers throughout the summer months. Towards autumn the animals again retire to the more saline regions of the total area of distribution.

Laboratory experiments, in which death rates were determined in two year old animals kept in different combinations of temperature and salinity, led to the conclusion that the salinity optimum depends on temperature. Increase of temperature caused the salinity optimum to shift in a downward direction. At a temperature of 20° C a salinity of ca. 29 $^0/_{00}$ proved to be optimal, whereas a temperature of 4° C corresponded to a salinity optimum of 33 $^0/_{00}$.

For one year old shrimps the salinity optimum at a temperature of ca. 20° C proved to be exceptionally low, lying in the neighbourhood of 15–20 $^0/_{00}$. Probably a relation exists between the low salinity optimum and the fact that during summer young shrimps penetrate farther into brackish waters than the older specimens.

A combined influence of temperature and salinity of quite the same character could also be demonstrated in newly hatched shrimp larvae. Moreover, the salinity limits for normal development of the eggs proved to be likewise dependent on temperature.

A similar influence of temperature and salinity was found in *Carcinides maenas* by BROEKHUYSEN (1936). It probably holds for a number of other Crustacea, in which a similar seasonal periodicity in distribution occurs.

It further appeared that, although in general low temperatures are more favourable than high ones, an extremely low salinity is relatively better endured when temperature is high. This fits in with the fact that in nature low salinities are inhabited only during the warmest months of the year.

Extremely high salinities (of about 50 $^0/_{00}$) also proved to be somewhat less unfavourable when combined with a high temperature. This is only of theoretical interest, however, as the highest salinity to be found in the southern North Sea little surpasses 35 $^0/_{00}$. In this salinity low temperatures are more favourable than high ones.

I tried to find an explanation for the above mentioned facts in a possible influence of temperature on the osmotic behaviour of the shrimp. To this end I examined, by means of conductivity determinations, whether temperature has any influence upon the osmotic concentration of the blood in animals kept in salinities ranging between 15 and 45 $^0/_{00}$.

Concerning the osmotic behaviour in general it could be proved that, although the concentration of the blood follows the concentration of the external medium to a certain extent, *Crangon* is generally able to maintain a certain difference in concentration between blood and medium. In salinities higher than 21–23 $^0/_{00}$ the blood is hypotonic, in salinities lower than 21–23 $^0/_{00}$ hypertonic in respect to the external medium.

As to the influence of temperature on the osmotic behaviour it could be proved that the difference between in- and external concentration (in hyper- as well as hypotonic animals) is greater at high than at low temperatures (see graph 20).

This result enables us to explain why extremely low or extremely high salinities can better be endured when temperature is high. We may safely assume that in general life is possible only when the internal concentration remains within certain limits. If the concentration of the external medium is steadily increased (or decreased) the upper (or the lower) admissible limit for the internal concentration will sooner or later be exceeded. As the difference between internal and external concentration always is greatest when temperature is high both limits will sooner be reached at a low than at a high temperature (see graph 20). In other words: there must be an extremely low and an extremely high range of salinities where life is possible only at a high temperature. Only the second case (extremely low external concentration) is of practical interest.

The next problem to be solved concerns the shifting of the salinity optimum when temperature is changed.

It could be proved that the internal concentration depends on salinity and temperature of the external medium. As it further appeared that certain combinations of salinity and temperature are more favourable than others it seemed plausible to regard the internal concentrations corresponding to these favourable combinations as optimum internal concentrations. These are for two year old shrimps the internal concentrations corresponding to *a.* an external salinity of 29 $^0/_{00}$ at a temperature of 20° C, *b.* an external salinity of 33 $^0/_{00}$ at a temperature of 4° C.

It could further be shown that the "optimum internal concentration" is not a fixed, but a variable value. Only the difference between internal and external concentration proved to be about the same in both situations. Consequently, this special difference (viz. the special degree of hypotonicity) and not the internal concentration itself seems to be the essential factor.

Meanwhile, the above mentioned facts and the inferences deduced from them are not sufficient to give a complete explanation of distribution and migration. During the winter months shrimps generally stay in regions where the salinity corresponds to the salinity optimum at the temperature prevailing there. When, during spring, the water temperature begins to increase the animals move to regions of lower salinity. However, this migration brings part of the animals to regions where the salinity is far below the optimum salinity at the temperature prevailing during the summer months. The maintenance of a special degree of hypotonicity, although of unmistakable benefit to the animal, is apparently not indispensable, as shrimps, notably the young specimens, evidently are quite able to live even in situations in which they are hypertonic. The penetration into more and more brackish water, which takes place during spring and early summer, can, in my mind, certainly not be explained from osmoregulatory necessity. With the migration towards more saline regions taking place during autumn things are otherwise, since a continued stay in regions of low salinity and at the same time low temperature would certainly have involved osmoregulatory difficulties.

In connection with the above a number of new questions arise, which, however, lie outside the scope of this investigation.

In the first place we can ask why the difference between in- and external concentration is greater at high than at low temperatures.

In the second place: what is the nature of the benefit arising from the maintenance of a special degree of hypotonicity?

Thirdly: which is the stimulus causing the animals to penetrate into salinities far below the salinity optimum at the prevailing temperature? It might be that the search for better feeding grounds plays a part in this.

Finally the question arises by what mechanism *Crangon* succeeds in keeping its blood in a state of hypotonicity. Hypotonicity was shown to occur in salinities higher than 23 $^0/_{00}$, hence it forms a most usual condition for the shrimp.

In this respect *Crangon* can be compared with *Eriocheir* (SCHOLES 1933, CONCLIN and KROGH 1938) and a number of grapsoid crabs (EDMONDS 1935), which show the same behaviour. Thus far, the mechanism by which hypotonicity is maintained is not known in any of these cases. KROGH (1938) suggests active secretion of salt ions against the concentration gradient, but in the case of *Eriocheir* no direct proof could be obtained.

The investigation was carried out at the Zoological Station of the "Nederlandsche Dierkundige Vereeniging" at Den Helder. I am greatly indebted to Dr. J. VERWEY, director of the Zoological Station, on whose initiative this investigation was started. His steady and lively interest throughout the work have assisted me a great deal in carrying it through.

I also want to express my gratitude towards Prof. Dr. E. H. HAZELHOFF for his valuable advice and for his criticism during the composition of this paper.

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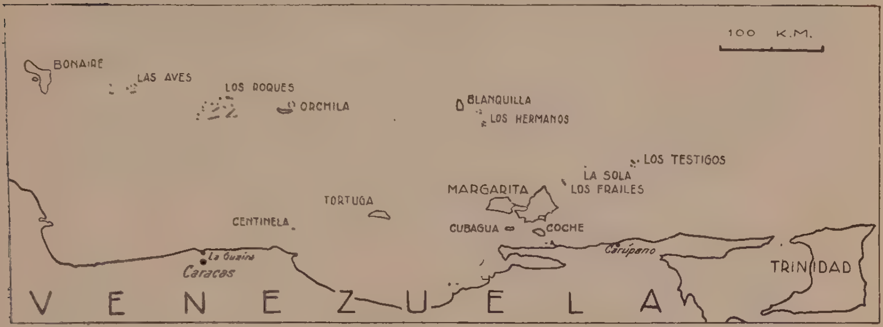

GORGONARIA VON VENEZUELA (INSELN BLANQUILLA UND LOS FRAILES)

VON

G. STIASNY.

RIJKSMUSEUM VAN NATUURLIJKE HISTORIE, LEIDEN

Dr. P. Wagenaar Hummelinck brachte von seiner letzten Fahrt nach Westindien und Venezuela (1936) eine kleine Sammlung von Gorgonarien mit, die mir zur Bearbeitung übergeben wurde. Die Stöckchen stammen von den venezuelanischen Inseln Blanquilla und Los Frailes, gelegen zwischen Trinidad und den niederländischen Inseln unter dem Winde. Das sind Fundorte, wo noch niemals vorher Rindenkorallen gesammelt worden sind. Schon wegen des Vergleiches mit der verhältnismässig gut bekannten Gorgonarienfauna des nicht weit entfernten Curaçao ist die Sammlung Hummelinck's nicht ohne Interesse. Sie enthält jedoch überraschenderweise nicht weniger als 4 neue Arten, was eigentlich kaum zu erwarten war, liegen doch die Inseln Blanquilla und Los Frailes in dem gleichen Stromgebiete wie die Insel Curaçao. Es zeigt sich deutlich, dass das ganze Gebiet in Bezug auf Gorgonarien noch viel zu wenig untersucht ist. Die meisten der neuen Species sind wohl nahe verwandt mit bekannten westindischen Arten, nur *Pterogorgia blanquillensis* weist Beziehungen auf zu *Pterogorgia australis* von der Torresstrasse, Golf von Manaar und Colombo, aber diese Ähnlichkeit ist wohl kaum anders wie als Konvergenzerscheinung aufzufassen.

Das Material befindet sich in vorzüglichem Erhaltungszustande. Sehr willkommen waren bei der Bearbeitung desselben die genauen Angaben, die HUMMELINCK fast bei jedem einzelnen Stöckchen über den Fundort und seine Facies, sowie über die Färbung der lebenden Tiere gemacht hat.

Die Sammlung, die sich im Besitze des Rijksmuseum van Natuurlijke Historie in Leiden befindet, besteht aus 17 Exemplaren, die sich systematisch in folgender Weise einteilen lassen.

Fam. **Plexauridae** Gray:

Plexaura wagenaari n.sp.	2	Ex.
Plexaura flexuosa Lam.	2	„
Plexauropsis flavida Stiasny	± 5	„
Plexauropsis puertorealis n.sp.	2	„
Eunicea hummelincki n.sp.	1	„

Fam. **Gorgoniidae** Ridley:

Pterogorgia acerosa var. *elastica* Bielsch.	3	„
Pterogorgia blanquillensis n.sp.	2	„

Auf die Fundorten verteilen sich diese Arten folgendermassen:

Puerto Real, Los Frailes, 18. VI. 1936; 3 m tief, auf sandigem Boden mit grobem Schutt; an der S.W.-küste der Insel, von den Wellen des Ostpassats geschützt. – *Plexaura wagenaari* n.sp., *Plexauropsis flavida* Stiasny, *Plexauropsis puertorealis* n.sp., *Pterogorgia acerosa* var. *elastica* Bielschowsky.

La Pecha, Los Frailes, 19. VI. 1936; 1½ m tief, auf felsigem Boden mit vielen Sand; an der S.W.-seite der Insel, vor den Passatwellen geschützt. – *Plexaura wagenaari* n.sp., *Plexauropsis flavida* Stiasny..

Playa Valuchu, Blanquilla, 21. VII. 1936; 3 m tief, auf einem reinen Sandboden mit verstreuten festen Gegenständen auf denen die Gorgonarien haften; in einer kleinen Bucht an der Südküste, die vor den vom Ostpassat aufgepeitschten Wellen völlig geschützt ist. – *Plexaura flexuosa* Lamouroux, *Eunicea hummelincki* n.sp.

Playa del Jaque, Blanquilla, 22. VII. 1936; 5 m tief, auf sandigem Boden mit grobem Schutt; an der S.W.-küste der Insel, vor den Passatwellen geschützt. – *Pterogorgia blanquillensis* n.sp.

Von Muriceidae findet sich auffallenderweise kein einziger Vertreter in der kleinen Sammlung.

Die Photographien für die Tafeln wurden, wie stets, von H. Cornet, Techniker am Rijksmuseum van Natuurlijke Historie, Leiden, mit bewährtem Fleisse und grosser Sorgfalt ausgeführt.

Dr. Hummelinck hat das Manuscript dieser Mitteilung durchgesehen und durch zahlreiche Bemerkungen über die Fundorte, Facies, Färbung der Stöckchen bereichert.

Fam. **Plexauridae** Gray

Gen. *Plexaura* Lamouroux

Plexaura wagenaari n.sp.

(Taf. I. Abb. 1–4, Textabb. A.)

2 Exemplare und zahlreiche Bruchstücke:

1. Los Frailes, La Pecha. 19. VI. 1936. ($MgSO_4$, Formol; Alkohol) „Schors licht roseachtig-grijs; polypen donkerbruin"[1]). Ein 140 mm langer, 8 mm dicker Ast ohne Basis, der sich gabelt. (Taf. I, Abb. 1).

2. Los Frailes, Puerto Real. 18. VI. 1936. ($MgSO_4$, Formol; Alkohol) „Schors licht groenachtig-grijs; polypen kastanjebruin; stam afgeplat."[2]) 4 Bruchstücke, Endäste, etwa 100 mm lang, 6 mm dick.

3. Los Frailes, La Pecha. 19. VI. 1936. (trocken). 2 Kleine Bruchstücke, eines davon gegabelt. (Taf. I, Abb. 2).

Gänzlich unverzweigt oder einmal gegabelt. Lange schlanke Zweige, die sich fast gar nicht verjüngen. Oberfläche glatt. Kelche allseitig stehend, 1–1½ mm weit von einander entfernt, bis 3 mm lang, unbewaffnet, vollständig retractil (Taf. I, Abb. 3). Die eingezogenen Calyces mit 8 Kerben. (Taf. I, Abb. 4). Viele dünne Längskanäle. Zenstralstrang schwach verkalkt, undeutlich gekammert. Stamm etwas abgeplattet. Coenenchym 2 mm dick, zweischichtig.

Spicula (Textabb. A): Aussen ein Panzer von plumpen Blattkeulen mit kurzen, breiten, glatten Blättern, kurzem Stiel, dicht, niedrig bewarzt (a, b, c, d, e) mit wenigen grossen Warzen besetzt (d), etwa 0.132 mm lang, mit langem, dicht, unregelmässig bewarztem Stiel (f), etwa 0.165 mm lang. Auch plattere Keulen mit seitlichen Fortsätzen, spitzzulaufendem

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[1]) Rinde hell rosafarben bis grau, Polypen dunkelbraun.

[2]) Rinde hellgrünlichgrau; Polypen kastanienbraun; Stamm abgeplattet.

Stiel, die Warzen manchmal zusammenfliessend (g), Doppelspindeln (h), unregelmässig dicht bewarzt, Spindeln (i, j), 0.198 mm lang, weniger dicht oder ganz regelmässig bewarzt (k), 0.10 mm lang. Alle durchsichtig, Innenschicht: mit dunkelvioletten, unregelmässig gezackten Sternen mit vielen kleinen (l) oder wenigen grossen (m, n) Warzen, oft ganz platt, etwa 0.132 mm breit; kleine stark eingeschnürte Spindeln mit glatten Stacheln, dickem Hals und wenigen Warzen, etwa 0.10 mm lang (o, p). Farbe grünlichgelblich, im Trockenpräparat die Kelche dunkeloliv-bräunlich; stellenweise schimmert die dunkelviolette Innenschicht durch den grünlichgelben Überzug.

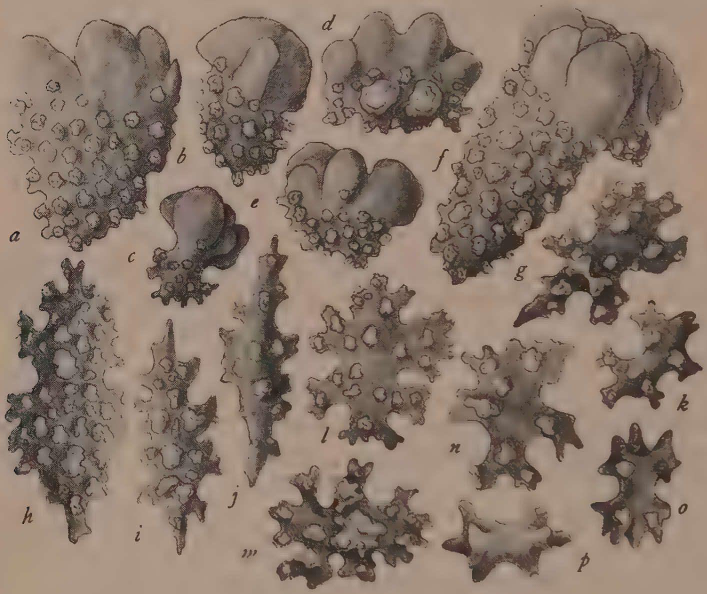

Abb. A. *Plexaura wagenaari* n.sp. Spicula.

In der Wachstumsform, den kleinen Scleriten, der violetten Innenschicht, stimmt die neue Art noch am besten mit *Plexaura ehrenbergi* Köll. von Westindien überein, bei der jedoch laut der Diagnose Kükenthal's (1924, p. 114) in der Rinde auch rote Spicula vorkommen (stimmt nicht mit der Bestimmungstabelle p. 111), was hier nicht der Fall ist, auch erreichen die Keulen nie die Grösse von 0.33 mm Länge. Kükenthal rechnet *P. ehrenbergi* zu den guten Arten des Genus *Plexaura*. Es liegt aber über dieselbe nur die ganz kurze Beschreibung **Ehrenberg**'s vor, der *Gorgonia antipathes* Esper (mit Abbildung) als synonym betrachtet, was aber **Kükenthal** nicht anerkennt. Sonst (**Kölliker**, **Moser**) wird die Art nur ganz beiläufig erwähnt, es gibt keine Abbildung der Wachstumsform, keine der Spicula. Und das soll eine gute Arte sein! Man kann ja gar nicht vergleichen! Es ist daher gar nicht ausgeschlossen, dass die vorliegenden Stöckchen trotz aller genannter Abweichungen doch identisch wären mit *P. ehrenbergi.*

Diagnose: unverzweigt oder gegabelt. Lange, schlanke, cylindrische Zweige, die sich nicht verjüngen. Oberfläche glatt. Kelche allseitig stehend, 1–1½ mm weit von einander entfernt, unbewaffnet, gänzlich retractil, bis 3 mm lang; wenn eingezogen mit 8 Kerben rings um die Öffnung. Viele dünne Längskanäle. Zentralstrang schwach verkalkt, undeutlich gekammert. Coenenchym 3 mm dick, zweischichtig. Dicke Aussenschicht mit massenhaften gedrungenen, plumpen Blattkeulen mit glatten Blättern, kurzem oder langem dicht bewarztem Stiel, 0.132–0.165 mm lang, Spindeln spitzzulaufend, unregelmässig, dicht bewarzt, 0.198 mm lang, alle durchsichtig. Innenschicht dünn, mit dunkelvioletten stark gezackten Sternen mit vielen kleinen oder wenigen grossen gezackten Warzen besetzt, 0.132 mm lang, kleine stark eingeschnürte Spindeln mit glatten Stacheln, wenig bewarzt, 0.10 mm lang. Farbe grünlichgelblich, Calyces bräunlich bis olivgrün. Violette Innenschicht stellenweise durchschimmernd. Fundort: Los Frailes (Venezuela).

Plexaura flexuosa Lamouroux, emend. Stiasny

Vergl. meine Ausf. 1935, p. 57/65, Taf. IV, Abb. 18, Taf. VII, Abb. 35, 36.

2 Exemplare Blanquilla, Playa Valuchu, 21. VII. 1936 (trocken).

1. 450 mm hoch, 250 mm breit. Fussplatte 40 mm breit. Ausserordentlich dicht verzweigter kräftiger Busch von schwarzbrauner Farbe. Stamm horizontal, mit einer Kalkkruste überzogen. 140 mm lang, 45 mm dick, erhebt sich plötzlich und verästelt sich sofort buschförmig. Endäste vielfach kugelig verdickt. Kelche flach, ohne Unterlippe.
2. 420 mm hoch, 310 mm breit, Basis 60 mm breit.

Von der ungewöhnlich breiten Basis, auf der auch das Stöckchen von *Eunicea hummelincki* aufsitzt, erheben sich ganz dicht nebeneinander stehend etwa 10 kleine Stämmchen, die einen sehr dicht verzweigten plattgedrückten aufrechten Busch von ovalem Umriss bilden. Endäste nur selten kolbig verdickt, meist schwach verjüngt abgerundet endigend. Kelche ganz flach. Dunkelschwarzbraun. In Westindien sehr verbreitete Form.

Die Exemplare fallen durch besonders dichte Verzweigung und die sehr breite Fussplatten auf.

Gen. *Plexauropsis* Verrill.

Plexauropsis flavida Stiasny

Vergl. Stiasny, 1935, p. 71/72, Taf. 1, Abb. 5. Textabb. S.; Stiasny, 1936, p. 17.

(Taf. I. Abb. 5, 6)

Etwa 5 Exemplare

1. Los Frailes, Puerto Real. 18. VI. 1936 (trocken). „Schors licht roseachtig-grijs. Polypen donkerbruin".[1]) (Taf. I, Abb. 5). 236 mm hoch, 170 mm breit, Fussplatte 32 mm breit.

Sehr dicht fiederig verzweigter aufrechter Busch in mehreren aufeinanderliegenden Ebenen. Von der breiten Fussplatte erheben sich zwei ganz kurze Stämmchen, die sich sofort in 3 oder 4 Nebenäste teilen, die fiederig angeordnete Seitenzweige tragen. Seitenäste bis 100 mm lang, dünn, cylindrisch. Hauptäste schwach abgeplattet. Kelche allseitig, dicht stehend, bräunlich-gelblich, eine Seite heller, die andere dunkel.

2. Los Frailes. La Pecha. 19. VI. 1936 (trocken). 400 mm hoch, 195 mm breit, Basis 35 mm breit.

Sehr dichter aufrechter Busch. Fast kein Stamm. 3 Hauptäste, die sich sofort fiederig verzweigen. Endzweige bis 140 mm lang. Oberfläche erscheint rauh. Kelche allseitig, dichtstehend. Sonst wie bei 1. Lichtgelb braun.

3. Los Frailes. Puerto Real. 18. VI. 1936. ($MgSO_4$, Formol; Alkohol).

Zwei kleine Bruchstücke (Astenden, fiederig verzweigt) mit teilweise gestreckten Kelchen. 100–110 mm lang. Grünlichgelblich.

4. Los Frailes, Puerto Real. 18. VI. 1936. ($MgSO_4$, Formol; Alkohol). „Schors licht roseachtig-grijs. Polypen donkerbruin."[2])

3 kleine Bruchstücke, Astenden, fiederig verzweigt, 100–120

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[1]) Rinde hell rosafarbengrau; Polypen dunkelbraun.

[2]) Rinde hellrosafarbengrau, Polypen dunkelbraun.

mm lang mit teilweise ausgestreckten Kelchen. 1 kleines complettes Stöckchen, 75 mm hoch, 22 mm breit, Basis 10 mm breit; mit kräftig ausgebildeten Kelchen. (Taf. I, Abb. 6).

Die schönen Exemplare stimmen ganz gut überein mit meiner Beschreibung eines nur mässig erhaltenen Stöckchens von Curaçao (1935, p. 71/2). Sie sind grösser, kräftiger, viel dichter verzweigt, die Kelche besser entwickelt. Die Oberfläche erscheint auf den Trockenexemplaren rauh. Keulen und Spindeln sind hier etwas länger als wie von mir angegeben.

Die Species *flavida*, von mir auf Grund eines einzigen nicht sehr gut erhaltenen Stöckchens nur mit Vorbehalt aufgestellt, wird bona species. Die Diagnose ist dahin zu ergänzen, dass die Polypen im Leben dunkelbraun sind, das Coenenchym rosa grau, beim Trockenmaterial mehr licht gelblich bräunlich, nicht nur citrongelb.

Plexauropsis puertorealis n.sp.

(Taf. I, Abb. 7, 8; Textabb. B)

2 Exemplare: Los Frailes, Puerto Real. 18. VI. 1936 (Alkohol).

1. 100 mm hoch, 35 mm breit, Fussplatte ca 5 mm breit.

Mehr minder in einer Ebene fiederig verzweigter, cylindrischer Stamm, 3 mm dick. Die Äste gehen nach verschiedener Richtung ab, alle sind kurz, unverzweigt und kaum dünner als der Stamm, am freien Ende schwach verdickt, abgerundet oder zugespitzt. Oberfläche körnelig. Kelche niedrig, völlig retractil, allseitig stehend, 1–1½ mm weit von einander entfernt. Achse dunkelbraun, Zentralstrang schwach verkalkt. Viele dünne Längscanäle. Grauweiss mit violettem Schimmer. Coenenchym zweischichtig.

Spicula (Textabb. B); Aussen ein Panzer von Blatt- oder Stachelkeulen, die Blätter in der Längsrichtung oder mehr seitlich orientiert, Stiel nicht dicht bewarzt (a, b, c), 0.198 mm lang. Stacheln ganz kurz, nur am Vorderrande aufsitzend, sonst ganz dicht unregelmässig rauh bewarzt (d), 0.264 mm lang. Breite gerade oder gebogene Spindeln (e, f), auf der einen Seite dicht, niedrig bewarzt, auf der anderen mit hohen Dornen besetzt, die selbst wieder kleine Dörnchen tragen, 0.231–0.33 mm lang. Alle durchsichtig. Innenschicht: schwach violett gefärbte, gerade oder gebogene, schlanke Spindeln, unregelmässig niedrig, rauh bewarzt (g, h), plumpere, weniger dicht

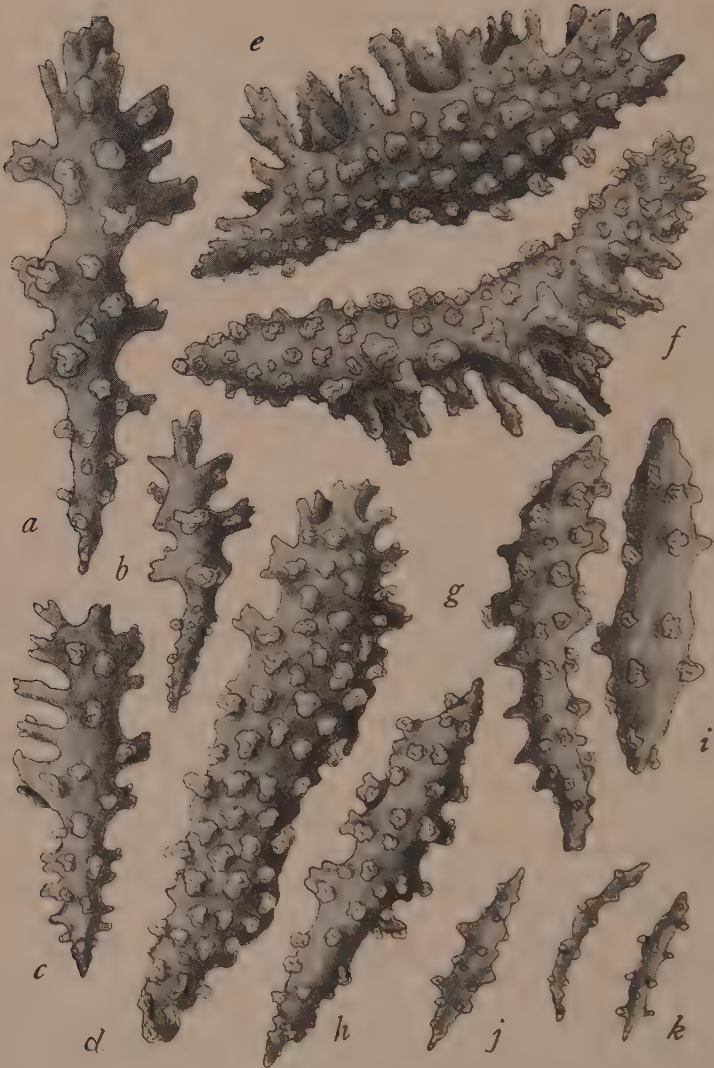

Abb. B. *Plexauropsis puertorealis* n.sp. Spicula

bewarzte plattere Spindeln (i), 0.198 mm lang. In den Kelchen kleine gerade oder gebogene Spindeln, wenig, niedrig bewarzt (j, k), 0.099 mm lang, durchsichtig.

2. 70 mm hoch, 32 mm breit, ohne Fussplatte.

Ein plattgedrückter fiederig verzweigter Busch, sonst wie 1. Farbe grauweiss.

Infolge der fiederigen Verzweigung steht die neue Art (sieh meine Übersichtstabelle der bekannten Species des Genus *Plexauropsis*, 1936, p. 17) der Species *flavida* von Curaçao nahe, die ja jetzt auch bei Los Frailes nachgewiesen ist. Sie ist viel weniger dicht verzweigt, kleiner, anders gefärbt, hat ganz anders geformte Spicula.

Diagnose: klein (etwa 100 mm hoch), fiederig verzweigt, Äste in verschiedenen Ebenen, alle kurz, unverästelt, nicht wesentlich dünner als der Stamm, am freien Ende oft schwach verdickt. Oberfläche körnelig. Kelche niedrig, allseitig stehend in 1–1½ mm Entfernung von einander. Zentralstrang schwach verkalkt, viele dünne Langscanäle. Coenenchym zweischichtig. Aussen Blatt- und Stachelkeulen mit langem Stiel, der wenig oder sehr dicht bewarzt ist, 0.198–0.264 mm lang. Gerade oder gebogene Spindeln, einerseits dicht, niedrig bewarzt, auf der anderen Seite mit hohen Dornen besetzt, die selbst wieder Dörnchen tragen, durchsichtig. Innenschicht violett, mit unregelmässig bewarzten, schlanken Spindeln, 0.198 mm lang. Kelchspicula kleine, wenig, niedrig bewarzte Spindeln von ca. 0.099 mm Länge, durchsichtig. Farbe grauweiss mit violettem Schimmer, besonders auf den Astspitzen.

Vorkommen Los Frailes (Venezuela).

Fiederige Verzweigung, Seitenäste in verschiedenen Richtungen abgehend, nicht dünner als der Hauptast, grauweisse Farbe sind die Hauptmerkmale der neuen Art.

Gen. *Eunicea* Lamouroux

Eunicea hummelincki n.sp.

(Taf. II, Abb. 9, 10, 11, 12, Textabb. C)

1 Exemplar mit 3 Stöckchen. Blanquilla, Playa Valuchu, 21. VI. 1936 (trocken), auf derselben Fussplatte als das 2. Stöckchen von *Plexaura flexuosa* Lmx.

Maasse:	100	mm hoch,	55	mm breit,	Basis	7	mm breit
	65	„ „	35	„ „	„	7	„ „
	150	„ „	37	„ „	„	8	„ „

Es liegen 3 Stöckchen vor, die dicht nebeneinander auf der mit *Plexaura flexuosa* gemeinsamen Unterlage aufgewachsen sind und bei oberflächlicher Betrachtung den Eindruck eines einzigen Stöckchens machen. Sie sitzen in einer tiefen Nische des Plexauridenstöckchens, das sie wie ein Mantel umgibt. Die 3 Stöckchen sind einander sehr ähnlich, nur sind sie verschieden hoch.

Kurzer Stamm, lateral dichotom in einer Ebene verzweigt. Alle Nebenäste nach aufwärts gerichtet, meist nur einmal gegabelt, nicht weiter verzweigt, nicht viel dünner (5 mm) als die Hauptäste. Endäste bis 80 mm lang. An den freien Enden zuerst etwas verdünnt, dann meist kugelig verdickt oder leicht angeschwollen, rundlich oder quer abgestutzt endigend (Taf. II, Abb. 10 und 11). Oberfläche feinkörnig, Kelche auch auf dem Stamme, allseitig, regellos verteilt, 1–2 mm weit von einander entfernt, relativ wenig zahlreich, 1–3 mm hoch, etwas länger als breit. In distalen Teilen sind sie höher als in den basalen, wo sie ganz flach werden können. Meist eine fast horizontale, vertikal auf die Astrichtung orientierte Röhre bildend mit

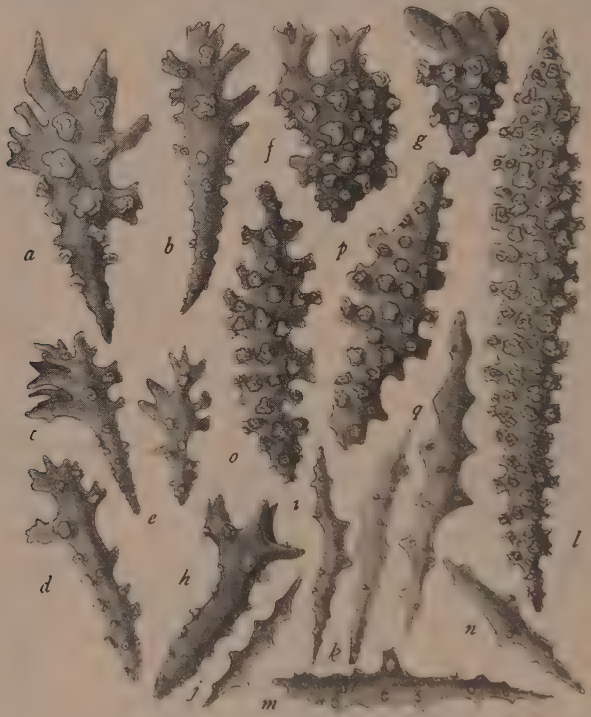

Abb. C. *Eunicea hummelincki* n.sp. Spicula.

schwach aufgebogener Unterlippe, während der obere Rand sich fast bis zum Niveau der Rinde herabsenkt. (Taf. II, Abb. 12). Kelchöffnung längsoval. Viele dünne Längskanäle. Zentralstrang gekammert. Coenenchym etwa 2 mm dick, dreischichtig.

Spicula (Textabb. C): Aussen: Stachelkeulen von sehr verschiedener Form (a–h), mit einfachen oder geteilten Stacheln, meist mit langem, dünnen, wenig bewarztem Stiel, bis 0.232 mm lang, mit kurzem, plumpem, dicht und niedrig bewarztem, breitem Stiel (f, g) 0.132–0.198 mm lang; durchsichtig.

Spitzige, dünne, wenig bewarzte Spindeln (i, j, k), sehr lange schlanke, dicht bewarzte Spindeln (1), 1.168 mm lang und länger. Mittelschicht mit breiten geraden oder leichtgebogenen, ziemlich dicht unregelmässig, rauh bewarzten Spindeln (o, p) durchsichtig oder violett, ± 0.168 mm lang, auch ganz schwach bewarzte, fast glatte, grosse Spindeln von ca 1 mm Länge (q). Innenschicht mit den gleichen Formen, aber auch noch gerade oder leicht gebogene, wenig, niedrig bewarzte, fast glatte Spindeln (i, j, k, m, n) ca 0.168 mm lang. Kelche mit kleineren schwach bewarzten oder niedrig bedornten Stäben, 0.09 mm lang, durchsichtig.

Farbe hellgelblich bräunlich, scharf contrastierend mit dem schwarzbraun der *Plexaura flexuosa*.

Die Art gehört in die Gruppe AII von Aurivillius (S. 231), die *calyculata* (Ell. & Sol.) und *succinea* (Pall.), beide von Westindien, umfasst.

Für die neue Species sind charakteristisch: die oft keulenförmig verdickten Enden der Zweige, die oft weitentfernt von einander stehenden, wenig zahlreichen Kelche, die vertikal von der Astrichtung abstehen und die schwach ausgebildete Unterlippe, endlich noch die grossen Stachelkeulen mit meist langem dünnem Stiel.

Diagnose: niedrig (etwa 100 mm hoch), lateraldichotom in einer Ebene verzweigt. Alle Nebenäste nach aufwärts gerichtet, nur einmal gegabelt, nicht weiter verzweigt, nicht viel dünner als die Hauptäste, am freien Ende zuerst verdünnt, dann meist kugelig angeschwollen. Kelche wenig zahlreich, 1–2 mm weit von einander entfernt, höher als breit, eine in rechtem Winkel zur Astrichtung abstehende Röhre bildend, mit schwach aufgebogener Unterlippe. Viele dünne Längskanäle, Zentralstrang gekammert. Coenenchym dreischichtig. Aussen Stachelkeulen mit langem dünnen wenig bewarztem Stiel oder sehr kurzem breiten dicht bewarzten Stiel, 0.232 mm lang; spitze, schlanke, wenig bewarzte Spindeln 0.198 mm lang, meist durchsichtig. Sehr lange dicht bewarzte Spindeln 1.168 mm lang und länger.

Mittelschicht: unregelmässig bewarzte breite Spindeln, durchsichtig oder violett, 0.170 mm lang. Innenschicht: gerade oder gebogene, wenig oder gar nicht bewarzte Spindeln, violett, 0.168 mm lang. Kelche mit kleinen, schwach bedornten Stäbchen, durchsichtig, 0.09 mm lang.

Farbe: hell gelblichbräunlich.

Vorkommen: Blanquilla (Venezuela).

Fam. **Gorgoniidae** Ridley

Gen. *Pterogorgia* Ehrenberg

Pterogorgia acerosa var. *elastica* Bielschowsky

Syn. bei Bielschowsky, S. 210. Deichmann, S. 199.

3 Exemplare

1. Los Frailes, Puerto Real, 19. VI. 1936 (trocken). „Schors licht groenachtig grijs, polypen kastanjebruin, mediaanlijn donker doorschemerend''.[1]) 180 mm hoch, 115 mm breit, 28 mm breite Fussplatte.

„Äste und Zweige hängen herab'', so steht es in der Diagnose von Bielschowsky. Die Photographie, pl. 5, fig. 23, zeigt sie aber alle nach aufwärts gerichtet und dies ist auch bei dem sehr gut erhaltenen Trockenexemplar der Fall. Die Kelche stehen seitlich nicht in 4 Reihen, sondern zumeist in nur ein oder zwei Reihen. Die Klammern mit lang ausgezogenen Enden sollten nur auf der concaven Seite Warzen tragen, aber hier sind solche mit Fortsätzen auf der konkaven und konvexen Seite vorhanden. Die Spindeln zeigen mehr den Typus derjenigen der var. *rigida* Bielsch. Die Farbe ist jetzt hellgelblich bräunlich, die Kelche sind als feine braune Punkte nur eben angedeutet. Mediane Längsfurche ziemlich tief.

2. Los Frailes, Puerto Real. 18. VI. 1936 (Alkohol).

3 Bruchstücke, fiederig verzweigte Endäste, bis 110 mm lang. Alle Endäste stark abgeplattet. Anthocodia gestreckt, stehen hier etwas weiter auseinander. Lichtgraugelb mit dunklem

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[1]) Rinde hellgrünlichgrau, Polypen kastanienbraun, Medianlinie dunkel hervortretend.

Mittelstreifen. Astspitzen mit violettem Schimmer. Spicula der Innenschicht auch violett.

3. Los Frailes, Puerto Real, 18. VI. 1936 (Alkohol).

1 Stöckchen, 130 mm hoch, 70 mm breit, Basis 20 mm breit. Kleines schönes Stöckchen, noch wenig verzweigt. Endäste herabhängend. Sonst wie 2.

Das Merkmal: „Äste herabhängend oder aufrecht'' ändert sich je nachdem Alkohol- oder Trockenmaterial vorliegt. Auch bei den beiden Alkoholpräparaten sind neben nur einseitig, auf der konkaven Seite bewarzten Klammern auch solche vorhanden, die Fortsätze auf beiden Seiten tragen. Dieses Merkmal hat, glaube ich, kaum jene Bedeutung, die BIELSCHOWSKY ihm in ihrer Differentialtabelle, p. 204, zuschreibt.

Die Revision der Arten durch BIELSCHOWSKY bedarf nach meiner Meinung dringend einer neuerlichen Revision.

Pterogorgia blanquillensis n.sp.

(Taf. 2, Abb. 13, 14. Textabb. D)

2 Exemplare; Blanquilla, Porto del Jaque. 22. VII. 1936 (trocken).

1. (Type) 320 mm hoch, 230 mm breit, Fussplatte 40 mm lang, 18 mm breit.

In mehreren Ebenen buschförmig verzweigt. Von der länglich-ovalen Fussplatte erheben sich 2 dickere, lange und ein dünnes, kurzeres Stämmchen. Die beiden ersteren sind fiederförmig verzweigt. Die Nebenästchen sind bis 120 mm lang, unverzweigt und verjüngen sich nicht, enden zugespitzt. Alle Äste sind nach aufwärts gerichtet. Proximale Teile schwach, distale stark abgeplattet. Oberfläche mit zahlreichen feinen Längsfurchen. Kelche klein, ganz flach, unbewaffnet, stehen stets seitlich dicht neben einander in einer oder mehreren Längsreihen, eine mittlere feingefurchte glatte Zone freilassend. (Taf. 2, Abb. 14). Viele dünne Längskanäle. Gelblichbräunlich mit violettem Schimmer. Achse schwarzbraun, Kelche dunkelbraun.

2. 420 mm hoch, 180 mm breit, Fussplatte oval, 30 mm lang, 15 mm breit.

Ganz kurzer Stamm, der sich in zwei fiederig verzweigte Äste gabelt; hier sind viele Nebenäste selbst wieder fiederig verzweigt. Viele feine Längsfurchen auf dem meist kelchfreien Mittelstreifen. Sonst wie 1. – Coenenchym zweischichtig.

Spicula (Textabb. D): Die äussere Rinde enthält nur durchsichtige Klammern, schwach gebogen, an den Enden stark bewarzt, alle Fortsätze nur auf der konkaven Seite, 0.10 mm lang (a, d), oder auf beiden Seiten (b, c, e), wenig rauh bewarzt. Die convexe Seite ist, wenn glatt, oft mit breiten, flachen, runden Höckern besetzt. Daneben Spindeln (f, g), regelmässig reihenweise oder unregelmässig bewarzt, an den Enden stets mit einem Büschel kleiner Warzen. Durchsichtig. In tieferen Lagen fast ausschliesslich Spindeln, meist regelmässig rauh bewarzt (h, i, j, k) und viele kleine unregelmässige Formen (einige Beispiele davon in l, m, n), die meisten violett, viele durchsichtig, 0.03–0.08 mm lang.

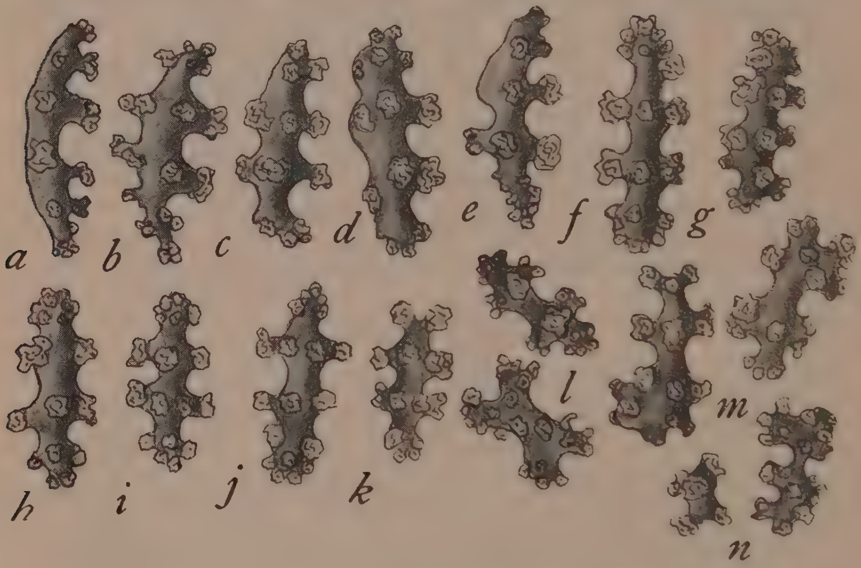

Abb. D. *Pterogorgia blanquillensis* n.sp. Spicula.

Die Art ist charakterisiert durch ihre dichte, fiederige Verzweigung in Buschform, Nebenäste auch selbst wieder gefiedert, Endzweige meist abgeplattet. Die Klammern tragen die Fortsätze mit den Warzen bald nur auf der konkaven, bald nur auf der konvexen Seite (was sie mit der *americana* nach DEICHMANN gemeinsam hat). Sie steht der Species *australiensis* (RIDLEY) von Torresstraits, Mannaar, Colombo noch am nächsten; mit *acerosa* hat sie gemeinsam, dass die Rinde aus zwei deutlich unterscheidbaren Schichten besteht.

Diagnose: In mehreren Ebenen dicht buschförmig verzweigt. Der ganz kurze Stamm teilt sich in 2 oder mehrere Äste, die fiederig angeordnete Nebenäste tragen, die oft selbst wieder fiederig verzweigt sind. Alle Äste und Zweige nach aufwärts gerichtet. Proximale Teile schwach, distale stärker abgeplattet, zugespitzt endigend. Oberfläche mit zahlreichen feinen Längsfurchen. Kelche klein, flach, rein seitlich stehend, in mehreren Längsreihen dicht nebeneinander, gelegentlich auch in einer Reihe auf den sonst kelchfreien Mittelstreifen. Viele dünne Längskanäle. Coenenchym zweischichtig. Aussen: schwach gebogene Klammern, an beiden Enden bewarzt, Fortsätze nur auf der konkaven Seite oder auch auf der konvexen, wenig, rauh bewarzt, 0.10 mm lang. Daneben Spindeln meist regelmässig rauh bewarzt, mit einem Warzenbündel an jedem Pole, durchsichtig. In tieferen Lagen fast nur Spindeln, regelmässig rauh bewarzt, 0.10 mm lang und viele kleine unregelmässige Formen, 0.03–0.08 mm lang. Farbe gelblich bräunlich mit violettem Schimmer. Kelch dunkelbraun. Fundort: Blanquilla (Venezuela).

Nachschrift.

Das Manuscript der vorliegenden Mitteilung wurde im October 1938 abgeschlossen. Durch ein Zusammentreffen verschiedener Umstände wurde die Drucklegung verzögert. Ich habe das Manuscript in seiner ursprünglichen Form gelassen und nichts daran geändert.

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TAFEL I

Abb. 1. *Plexaura wagenaari* n.sp. Habitusbild. Gegabelt. Äste cylindrisch. grünlichgelblich mit violettem Schimmer.

Abb. 2. *Plexaura wagenaari* n.sp. Astende nicht verjüngt, cylindrisch. 5 ×

Abb. 3. *Plexaura wagenaari* n.sp. Astende mit gestreckten Kelchen. Alkohol. 6 ×

Abb. 4. *Plexaura wagenaari* n.sp. Astende mit eingezogenen Kelchen. Trocken. 6 ×

Abb. 5. *Plexauropsis flavida* Stiasny. Habitusbild. Sehr dicht fiederig verzweigter Busch. Gelblichbräunlich.

Abb. 6. *Plexauropsis flavida* Stiasny. Astende. Rauhe Oberfläche. Trocken. 5×

Abb. 7. *Plexauropsis puertorealis* n.sp. Habitusbild. Fiederig verzweigt. Grauweiss.

Abb. 8. *Plexauropsis puertorealis* n.sp. Detailaufnahme des distalen Teiles. 6 ×

TAFEL II

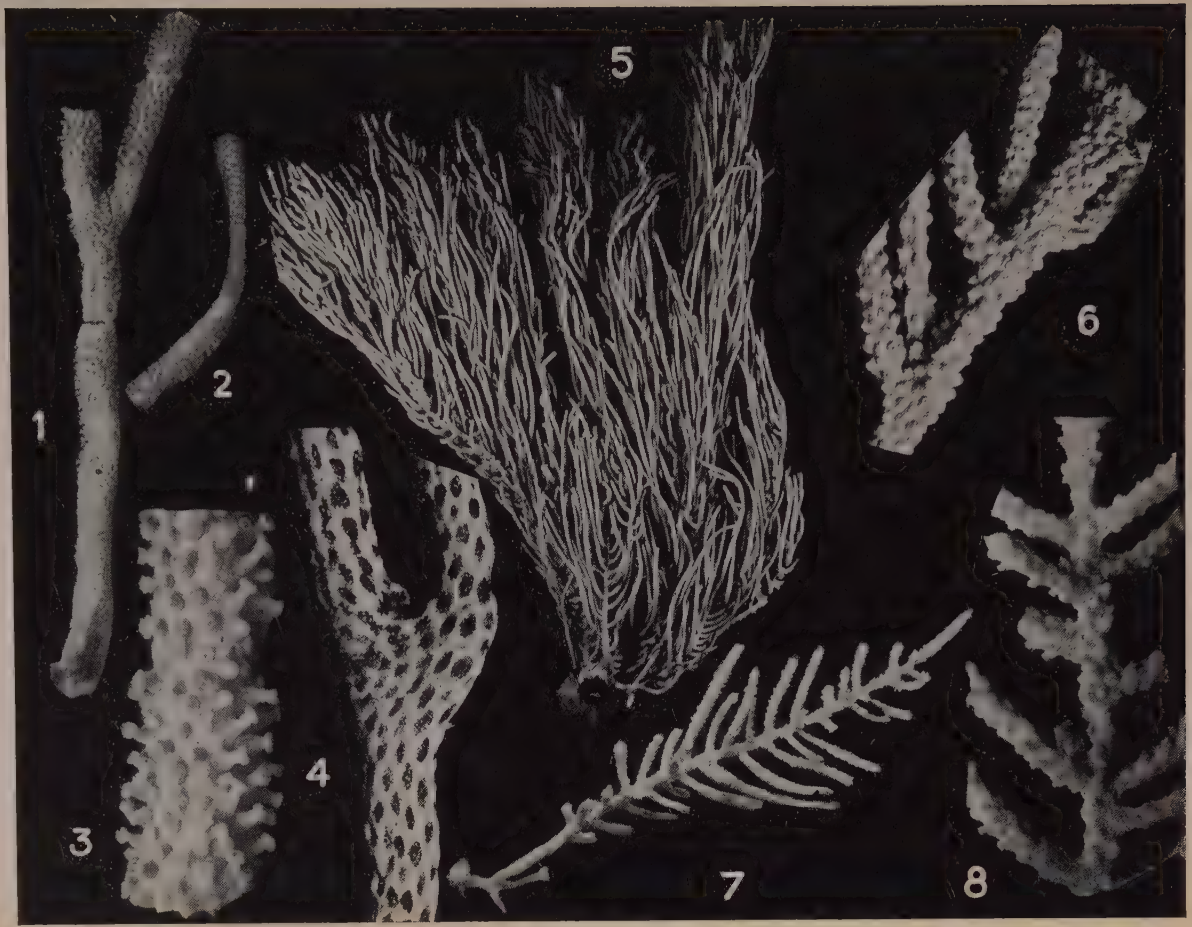
Abb. 9. *Eunicea hummelincki* n.sp. Habitusbild. Das Stöckchen sitzt auf gemeinsamer Basis neben *Plexaura flexuosa*. Hellgelblichbräunlich.

Abb. 10 und 11. *Eunicea hummelincki* n.sp. Zwei Endästchen kolbenförmig verdickt. 6 u. 8 ×

Abb. 12. *Eunicea hummelincki* n.sp. Detailaufnahme aus mittlerer Höhe- Kelche röhrenförmig, vertikal abstehend, mit kurzer aufgebogener Unter. lippe. 6 ×

Abb. 13. *Pterogorgia blanquillensis* n.sp. Habitusbild. Dicht buschförmig fiederig verzweigt. Gelblich bräunlich mit violettem Schimmer.

Abb. 14. *Pterogorgia blanquillensis* n.sp. Detailaufnahme aus mittlerer Höhe. Kelche seitenständig. Zahlreiche Längsfurchen. 6 ×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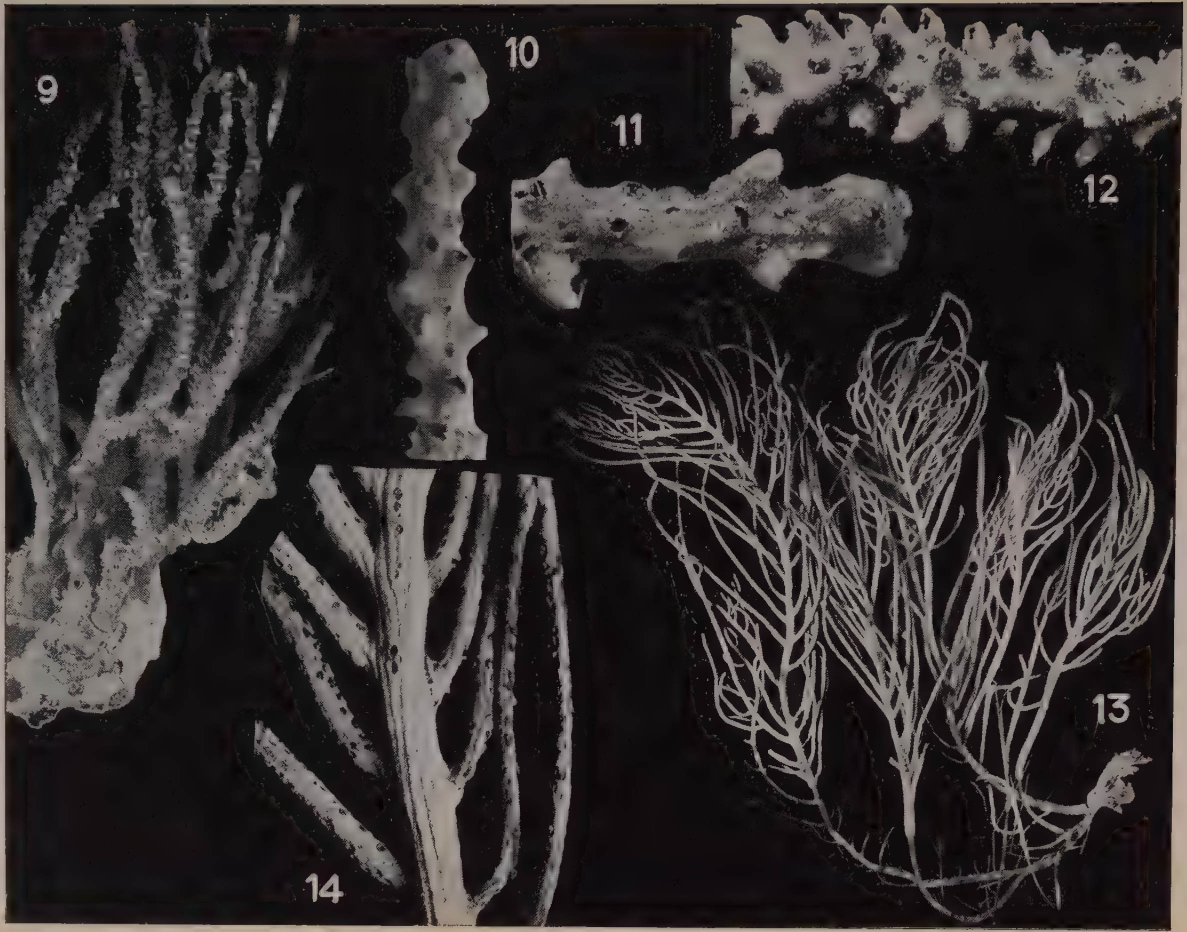
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ON THE DISTRIBUTION OF MUSSELS ON THE INTERTIDAL SAND FLATS NEAR DEN HELDER

BY

D. J. KUENEN

ZOOLOGICAL STATION, DEN HELDER

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INTRODUCTION

The aim of the investigations to be described in this paper was to understand what factor or factors might be responsible for the distribution of *Mytilus edulis* L. on the mud and sand flats near the harbour of Den Helder.

Though I originally intended to study all factors which might exert an influence it became clear during the investigations that this would cost too much time. Although much still remains to be done I thought it worth while to publish the results at this stage. I restricted myself to four factors, three of which seemed to be most prominent, current influence, substratum and food. The fourth, oxygen, was studied only superficially. As the factors substratum, food and oxygen are all dependent upon water movements the currents were considered of prime importance and attention was in the first place directed towards them.

Although only a small area was considered in detail it was hoped that the results might throw some light on the distribution of *Mytilus edulis* as a whole.

The observations and experiments were made in the summer months of 1935, 1936 and 1937 under the supervision of Dr J. Verwey, Director of the Zoological Station at Den Helder, to whom I am very much indebted for his continuous help during the experiments and the preparation of the manuscript.

DESCRIPTION OF THE FLATS AND THE MUSSEL BEDS

The flats in question lie opposite the Zoological Station, Den Helder, east of the harbour (see map, fig. 1). They have grown up between two stone dams, which border them on approximately south and west side. The western dam (Leidam) borders the harbour, while the second dam (Vangdam), which is much longer, but a great deal lower, has the function of forcing part of the ebb and flood water through the harbour by acting as a barrier. In this way the harbour is kept at sufficient depth by natural means. This second dam is 3.3 km long, but the flats along its northern side emerging at low water reach a length of about 1.8 km only. Along their northeastern side the flats are bordered by a creek, which runs further along the Vangdam and transports the water round its eastern end. At its northern

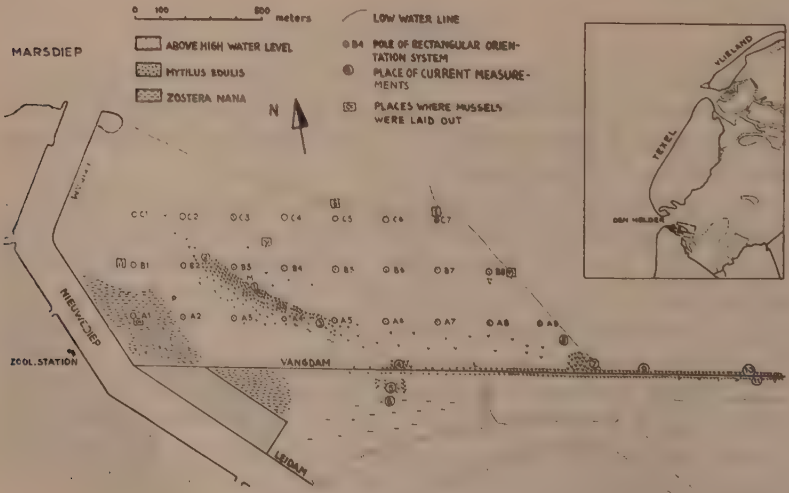

Fig. 1.

end this creek discharges into the Malzwin, one of the deeper creeks of the Waddenzee. The Malzwin runs along the northern side of the flats and discharges into the Marsdiep just opposite the entrance of the harbour of Den Helder.

The western parts of the flats are highest and the extreme corner where the two dams meet is only submerged at high water springs. From there the flats gradually slope off towards the east and north to just below low water springs. After that they fall off much more steeply into the creeks running along them. Along the creek on the northeastern side runs a slightly elevated sandridge. Some very shallow creeks and pools are to be found on the flats. The pools retain their water during the period of ebb or drain slowly, while the creeks form a not very well marked system, which carries the water to and from the highest parts of the flats, especially just before and shortly after total submergence and emergence. When the tide has risen the creeks lose much, though not all of their significance.

The details of the morphology of such flats do not remain unaltered for a long time and apart from gradual changes the aspect may suddenly be altered to a large extent by storms. The flats are probably still growing upwards, as they have been doing ever since the dams were built. A more rapid change

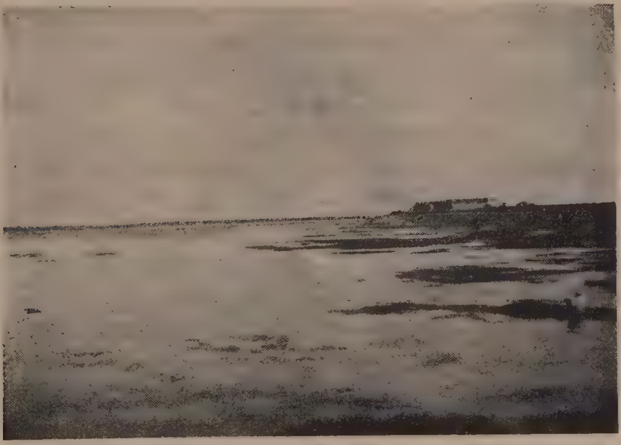

Fig. 2. Showing the limit of the *Zostera* area, which is the softest part of the flats, looking SE. A2 should be visible. The houses in the background are on the trapezium-shaped enclosure between the dikes (see map).

which could be observed in later years was probably due to the building of the main dike closing the Zuiderzee. It was finished in 1932, and while the amplitude of the tides became larger the currents increased in strength, especially in the neighbourhood of Den Helder. This resulted in a deepening of the creeks. The dam along the harbour was formerly never submerged, but owing to the same cause this has occurred occasionally recently during heavy storms. The Vangdam is highest where it joins onto the Leidam, but even there it is much lower than the Leidam. Its lower eastern part is submerged at every high water and only seldom does not emerge at low water (strong westerly winds). The part of the Vangdam west of L (see map) lies between high water neaps and high water springs.

The flats themselves are rather bare. Their highest part, in the corner where the two dams meet, bears a rather luxurious vegetation of *Zostera nana* Roth. (fig. 2), and in the creeks of this part grows some *Zostera marina* L. *Chaetomorpha linum* Kütz. and *Ulva lactuca* L. can regularly be found here. The flats themselves may in certain periods bear a covering of *Enteromorpha* and other algae. Further a small ridge of sparse growth of *Zostera nana* occurs just behind (west of) the major mussel beds, and a poor vegetation of *Fucus spiralis* L. is found on many of the clusters of mussels and the mussel beds.

Everywhere on the flats we can occasionally find mussels, but their numbers are mostly small. There is one area, however, which is quite covered by them and which first drew attention to the problem to be investigated later (fig. 3). This area forms a band which traverses the flats in an approximately northwest-southeast direction (see map). It is characterized by a series of large mussel beds, the largest of which measure about 8 × 4 m. On their southwest side the mussel beds become smaller and smaller and after they have become no more than a few widely scattered clusters they gradually disappear. Towards the northeast the beds are abruptly bordered by the bare flats without mussels. One or two small beds, overgrown with *Fucus spiralis*, and small clusters lying about can be found further out, but they never hold out for any length of time and are generally soon washed away.

There is a small area on the eastern extremity of the flats, where the creek and the Vangdam meet, which is again covered with mussels. Further, two small beds of mussels occurred in 1935

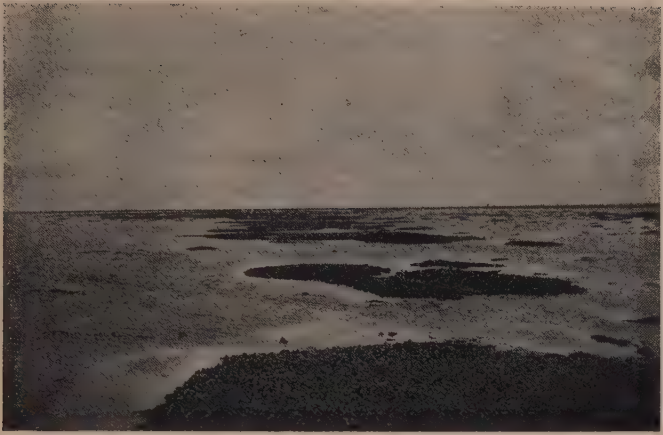

Fig. 3. Largest mussel beds near M, looking SE from near B3.

north and south of the Vangdam near A6, but during 1936 and 1937 they gradually disappeared entirely.

On the eastern side of the Leidam no mussels can be found. On the Vangdam mussels occur from about A5 onward. At first they are few and extremely small, but as we proceed their number and especially their size increases. From the point where the flats on the north side end the mussels cover the dam almost completely. This part of the dam has a number of breakwaters on its northern side, which are covered completely with mussels. At the south side of the dam the mussels have grown out over the flats. As they have apparently been collecting mud for a long time the beds have been raised to a much higher level than the surrounding flats, and they are nearly as high as the dam itself. It therefore looks as if the dam were about one and a half time as wide as it really is. Now it is very remarkable that behind each breakwater the mussels extend further over the flats than in between the breakwaters. Moreover, the mussels on the dike between the breakwaters are confined to the narrow grooves between the stones or very nearly so, whereas behind the breakwater the dam is quite covered by them. A further influence of the breakwaters appears from the occurrence of a low and sparse vegetation of *Fucus spiralis* on the middle part of the dam, but only in between the breakwaters (fig. 4). It seems as though the

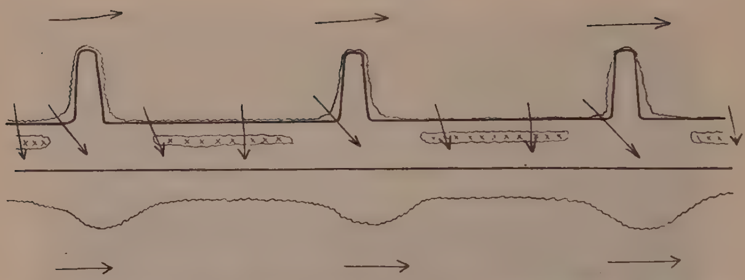

Fig. 4. Diagrammatic representation of the situation near 10 and 11. The areas with the crosses show the parts where *Fucus spiralis* is found. The mussel beds extend over the flats south of the dike, especially behind each breakwater. The arrows show the direction of the incoming tide just after the dam has become submerged. The chief current still runs, and remains for a long time running, parallel to the dike.

strong currents in between the breakwaters, as compared with behind them, cause these differences.

OBSERVATIONS AND EXPERIMENTS

The first point to consider as an explanation of the distribution which has just been described would of course be the dispersal of the larvae. I do not think, however, that his factor can be of much importance. The young mussels are planctontic for some time and consequently they will spread over a considerable area. Their distribution will be universal, though not necessarily even, over the entire area and we cannot imagine that they would not reach any point of these flats. As they will fix themselves to any object (Coe, 1932) and even settle on very soft mud (Wohlenberg, 1937) they can settle on all parts of the flats. The dispersal and the settling of the young mussels cannot therefore explain the peculiar distribution of the adult mussels.

In some cases enemies have been found to play an essential part in the distribution of mussels. American authors specially mention *Asterias vulgaris* and *A. forbesii* as a dangerous enemy of *Mytilus edulis* (Field, 1922; Newcombe, 1935). *Asterias rubens* L., which might play the same part in the distribution of this same species of *Mytilus* in European waters (cf. Havinga, 1929), cannot be of any importance here, as we are only considering the distribution within the intertidal zone, and the starfish does not occur there in any quantity. There also seems to be no reason why gulls or any other predators should eat the mussels from one place and leave them in another.

General observations and considerations led to considering one factor as the most important in influencing the distribution of the mussels over the flats. The occurrence of mussels on the stone dam and on the concrete poles on the sands, and the fact that they did not occur on the sand just beside these places, their absence on the east part of the dam between the piers and their occurrence in the shelter of them, and in fact all that could be seen here and what is known about mussels generally, made it probable that currents, especially in combination with the condition of the substratum, had a primary influence on the distribution of the mussels.

It seemed, therefore, that much would be gained by measuring the currents in some detail in different places, both where mussels were to be found and where they did not occur, to see if some correlation could be found between their occurrence and some characteristic of the prevailing currents.

In direct connection with this work investigations as to the influence of the substratum would have to follow. It will be shown that these factors cannot fully explain the observed distribution, and that a further factor, namely food supply, will have to be considered to complete the picture which has been formed of the reigning conditions on the flats.

1. CURRENTS

Fig. 5 shows the direction of the incoming tide. The length of the arrows is more or less proportional to the strength of the current. The dotted arrows show the direction of the currents after the dam has become submerged. It should be understood, however, that the data of fig. 5 are not like those described below based on measurements, and that therefore direction and length are only approximately right.

The current measurements had to be made in shallow water and often with very low current velocities. For that reason current meters could not be used and I therefore adopted the much simpler way of timing floating seaweed. This was done in the following way:

A piece of bamboo of exactly 2 m length was fixed rectangularly onto another stick so that the first could be held horizontally in

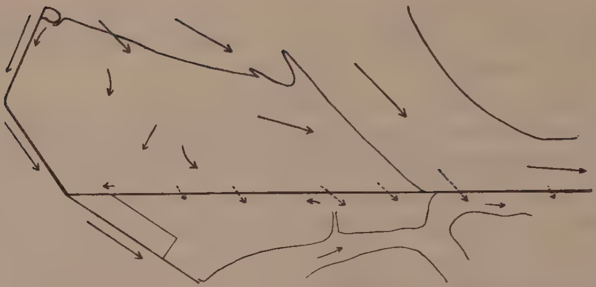

Fig. 5. Showing the direction and approximate relative velocities of the flood current over the flats. The dotted arrows show the direction of the currents after the dam has become submerged.

the water. It was placed in the direction of the current, the water flowing along it from one end to the other. A piece of *Fucus vesiculosus* or *Ascophyllum nodosum* was then thrown into the water beyond the end of the stick upstream, and timed with a stopwatch as it floated along the length of the stick. Three readings were taken directly after each other, and the mean of these was taken. This was repeated every quarter of an hour. The method is quick and accurate as long as there is not too much wind. When the strength of the wind was more than 5 (scale de Beaufort; 8.6 m/sec.) no measurements could be made with any accuracy, as the direction and the velocity at the surface and nearer the bottom then greatly differed. This could be shown by throwing into the water strands of *Ascophyllum*, which then took up an oblique position owing to the difference in the currents.

At the point where the current was to be measured a pole was driven into the bottom, and a boat or canoe was fastened to it, from which the currents were measured every 15 minutes during the period of submersion. In this way a curve of the current velocity as a function of time could be constructed (fig. 6). Each curve has two maxima, one for the incoming and one for the outgoing tide (the direction is not incorporated in the diagram). The currents of the incoming tide are often stronger than those of the tide running out. LÜDERS (1930) found this to be the rule in the German Waddenzee (Jade bay).

The minimum at high water is often not 0, as the current turns round 180° gradually and does not come to a full stop. The time of exposure is not given exactly, but is, of course, about 12^h20 minus the time of covering. Currents were measured at or near neap as well as spring tide and with different wind directions.

The following places were taken for measurements (see map fig. 1):

1. Mussel beds at the point where they were largest, halfway between B3 and A4;
2. between B2 and B3, where only a few small clumps of mussels grow;
3. between A4 and A5, and like 2, near the extremity of the mussel beds;
4. the small beds beside the dike near A6 (1935 only);
5. the beds beside the dike at the opposite side of 4 (1935 only);
6. on the flats near 5, outside the shallow creek which runs along the dike here; no mussels;
7. on the triangular bed on the east corner of the flats;
8. on the sandy ridge bordering the flats on the east side; no mussels;
9. on the dike, at 2000 m from the harbour;
10. on the dike, at 2400 m from the harbour;
11. just behind the dike a few meters further along, where the mussels have spread some way over the muddy flats at the south side.

While measuring the currents it soon appeared that a complete picture could not be arrived at in the time at my disposal, for several reasons. In these shallow waters the wind has a great influence on the strength of the current, the time of covering, and even on the direction of the current. Two measurements in the same place made two days running may show considerable differences with even little difference in wind. A further difficulty was that the period of submersion of course only coincided with daytime at certain intervals. What I needed were the velocities of the flood and ebb currents during the period of submergence, each period of submergence being separated from the next by a period of emergence. If the outgoing tide occurred in the morning and the incoming tide in the evening these two parts had to be joined together to form a curve of the whole period of submergence. This joining together (in converse order) could best be done at the moment of high water. It was very difficult and often impossible, however, to determine the moment of high water when watching the current, as it very seldom stopped and then started flowing in the opposite direction, but as a rule turned round gradually. Besides, in those places where the tide did not turn round there sometimes was a more or less long period of practically stagnant water. The official time of high water, as given in the tide tables, was of no use, as the winds often influence the tide to such an extent as to change the time of high water considerably. The only way that seemed practicable was to take the moment of high water as registered by the tide gauge in the Marsdiep. It appeared, however, that even then there was a great difference in time on two different days between the moment of high water in the Marsdiep and, for instance, the moment the water started covering a certain mussel bed.

These and many other factors influence the results to a greater or smaller extent, and we have to consider them with some reserve. In my opinion, however, the conclusions drawn from the measurements are justified.

There are two values which interest us most of all. In the first place there is the maximum current velocity. It is quite possible that this factor influences the distribution of the mussel, as it may be expected that above a certain value the currents sweep the mussels away. This would, of course, only refer to high current velocities. The second value of interest is the value in which is expressed both the strength of the current and the time during which it is in operation. It is possible that a short spell of strong current is equalled in its influence by a long time of a less strong current. Besides, the entire time of submergence as compared to the time of emergence is a factor of great influence, which should be expressed in the second value also.

Now, as regards the first value, the maximum current velocity was probably never measured at any place, as I made only few observations on each place, and stormy days, on which the currents are certainly the strongest, were never used for measurement (see above). The second value, however, could be best expressed in the following way, which gave us the relative values for the mean current velocity. The mean current velocity in a certain place per $12^{h}20^{min.}$ is proportional to the area enclosed between the curve and the horizontal axis (see fig. 6). The best way to arrive at the relative values of these areas is to add up the ordinates of every quarter hour, which means adding up all the measured values of one tide. Comparing the sums from different places we compare the relative values for the mean current velocities at these places. From the different measurements on the different days a mean could be calculated for each place of measurement, which I will call, for convenience sake, the „current figure''. Now this value, to a certain extent, also indicates the relative value for the maximum current, for it could be seen from the measurements that a place with a high mean of total current (= current figure) also had a high maximum. This of course is natural, because in the northeastern part of the flats the water runs faster, but also the time of covering is longer than in the southwestern parts, where both the current velocity and the duration of the covering are much less.

The results of the current measurements, expressed as current figure, are given in Table I, while in fig. 6 an instance is given of a measurement from each locality.

Fig. 6*a*: localities 1, 2, 3. At 1 there is a stronger current than at 2 and 3, which lie near to it. This is due to the fact that the mussel beds here occur in a shallow creek, which takes the water to and leads it from a great part of the mud flats, where the *Zostera* vegetation can be found. As we see, the difference chiefly exists in the beginning of the flood and the end of the ebb. Before and after the time of high water (in this case from 4^h to 6^h30) there is hardly any current at all, most of what there is being due to the wind. Here it was easy to join the two curves together, the ebb having been measured in the morning and the flood in the evening.

Fig. 6*b*: localities 4, 5. These two points, like 1, are situated in shallow creeks. The curve for 4 is an instance of two parts of a curve not joining well together (between 3^h and 4^h15). There is no difficulty with the curve for 5. The strange changes in current velocity (and direction) between 6^h and 8^h30 are due to the wind, which apparently often has much influence on the currents at these places. The joining of the curves in this case was not done at the moment of high water, which occurred probably about 6^h.

Fig. 6*c*: localities 5, 6. Another curve for 5 is given here, the measurement having been made at the same time as at 6. This last point is situated on the muddy flats close by. It was a windless day and the turning round of the current at locality 5 (9^h) appears to be normal, as the water first drains over the flats directly (southwest and west), but afterwards, as the flats begin to emerge, has to run eastwards along the creek beside the Vangdam. The moment of highwater was about 6^h, which, however, cannot be seen from the current velocity.

Fig. 6*d*: localities 7, 8. At 7 we find mussel beds; at 8 the bare sand is distinctly ribbled. The currents are much stronger at 8. As we see, the tide here turns round (5^h45) and does not come to a full stop.

Fig. 6*e*: locality 9. Where the flats end the dike bends the current round, and as soon as the level of the water has risen above that of the dam the

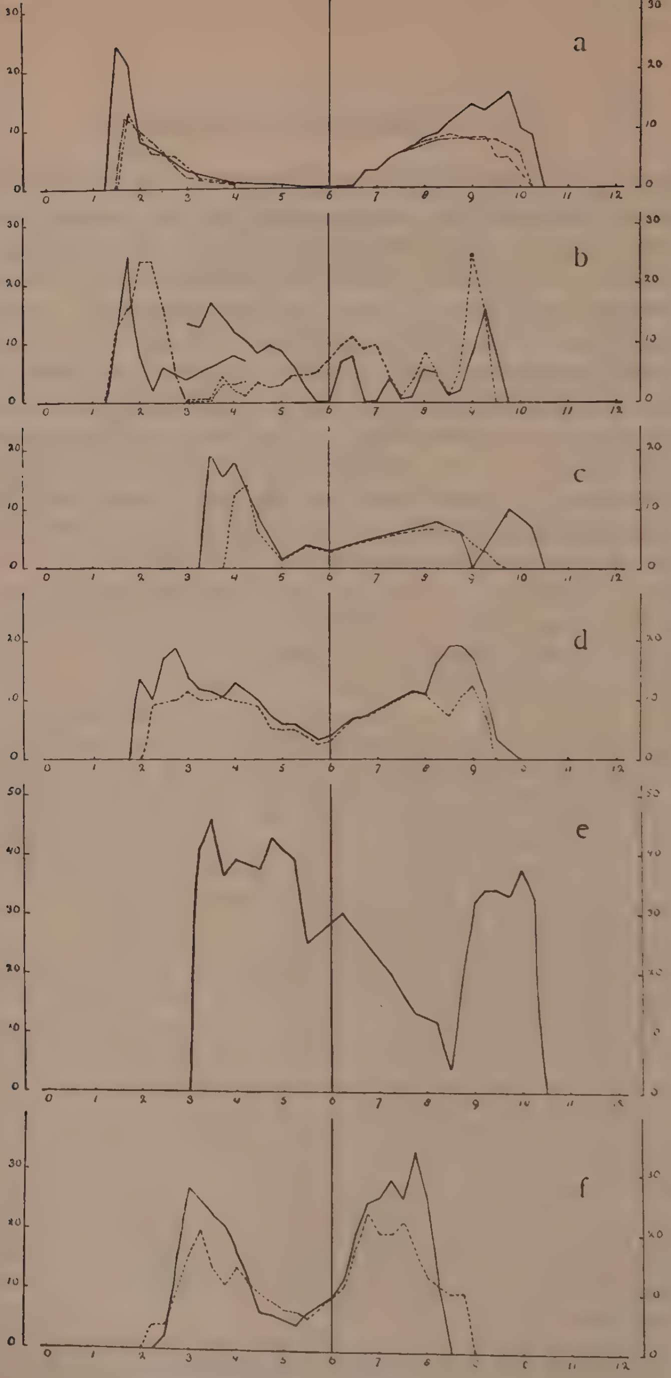

Fig. 6. Current curves for different places (see map). Horizontal axis = time in hours; high water in the Marsdiep reckoned as 6ʰ. Vertical axis = current velocity in meters per minute. Left half of each figure = flood, right half = ebb. *a.* 14 VIII 35. ——— = 1, ------ = 2, -·-·-· = 3. *b.* 19–20 VIII 35; 19 VIII: second half of flood and entire ebb; 20 VIII: first half of flood. ——— = 4, ------ = 5. *c.* 21 IX 35. ——— = 5, ------ = 6. *d.* 27 VII 36. ------ = 7, ——— = 8. *e.* 5 IX 35. ——— = 9. *f.* 20 VIII 35. ——— = 10, ------ = 11. For further discussion of the figures see text.

water runs obliquely over it. The current is very strong. A peculiar influence of the wind is shown here, as the current turns round very late (8^h30), 2½ hours after high water in the Marsdiep. As observation at the time showed the water had already been falling for some time. This is also shown by the shortness of the period of ebb.

Fig. 6*f*: localities 10, 11. The current here runs more parallel to the dike and therefore its strength over the dike is not as great as at 9. The influence of the breakwaters at the north side of the dam is obvious, as the current behind them (11) is much less strong than between them (10). The early change in the direction of the current (5^h15) and the high velocity of the ebb current are probably both due to the wind.

TABLE 1

	A	B	C
1. (3)		199–**264**–294	
2. (3)	155–**171**–199		
3. (3)	154–**180**–217		
4. (4)		201–**230**–263	
5. (5)		173–**252**–301	
6. (1)	122 (178) *)		
7. (4)		171–**217**–287	
8. (2)	302–**356**–409		
9. (4)			521–**697**–874
10. (2)			387–**406**–425
11. (2)		288–**295**–303	

Lowest, mean, and highest value for the current figure in different places of the flats (1–11). A = no mussels, B = mussel beds, C = on the dike. The number of days on which measurements were made is given in parentheses after the locality number.

*) For 6 only one measurement was made on a day of neap tide, amounting to 122 as current figure. The value is probably very low. That same day the figure for 5 was 173. The mean for 5 from 5 measurements was 252, and the mean current figure for 6 will therefore be higher in approximately the same relation, amounting to 178.

If we look at the value for the current figure more closely we see that there is some correlation between this value and the presence of mussels. When the current figure is less than 200 the circumstances are apparently not favourable for the growth of the mussels (localities 2, 3, 6). Where the figure is 200 to 300 mussels are found (localities 1, 4, 5, 7, 11). Where the current figure is above 300 we do not find any mussels on the flats (locality 8). On the stone dam, however, currents can be much stronger without any apparent harm to the mussels (localities 9, 10).

On the flats, therefore, a certain mean value of the current figure corresponds to the occurrence of mussels, whereas on the stone dam, as far as we can see from these measurements, this is not the case.

Now, from these data alone it is not possible to conclude whether it is the mean or the maximum current running at a certain place, which is the essential factor in the distribution of the mussel. As far as the outer parts of the flats are concerned it seemed probable that it was the maximum current velocities which made life impossible for the mussels, and it seemed worth while to make some experiments to show this.

Mussels were laid out on the flats at different places. These places, which are marked on the map (fig. 1, γ, δ, ε, η), were all situated on the hard sandy parts of the flats. An area of 75 × 75 cm was selected and 400 mussels were laid down there. Fig. 7 gives an instance of the way in which this was done in all the places.

γ. The mussels were put down at low water. After one day most of them had joined together in clumps. After three days they were washed away to some distance and only about 200 remained on the original area (fig. 8). After 12 days about 100 remained

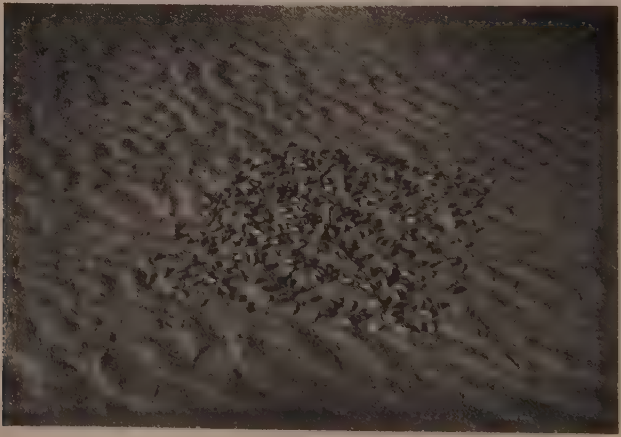

Fig. 7. η. Showing 400 mussels as they were put out on the different places. They are all separated from each other and the area covered is about 75 × 75 cm. Photograph taken immediately after they had been put down.

Fig. 8. γ. Mussels after 3 days on the sands. All those remaining on the original place have fixed themselves onto another mussel.

and 225 were counted up to a distance of 6 m. They were all washed along in the direction of the flood current. After 14 days only few remained on the original area (together with 27 which had attached themselves to the little post marking the original place) and 132 were found within 6 m distance. After 17 days

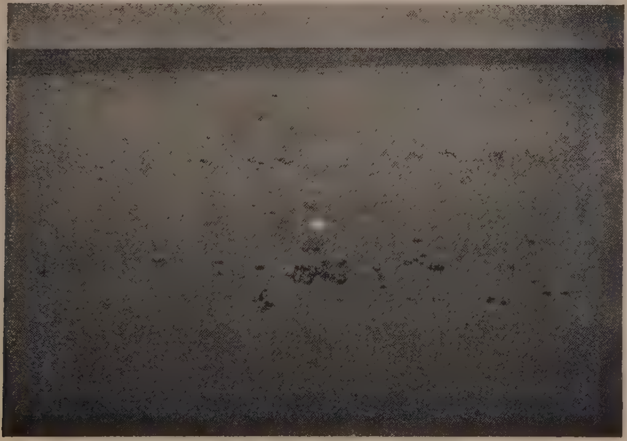

Fig. 9. δ. Mussels after 3 days on the sands. On the background the Malzwin.

there were only 15 on the post and 49 within 6 m. When inspected 5 weeks later not a single one was to be found.

δ. At γ every tide left the mussels exposed for some time. The position of *d* was a little lower, being about between the low water mark of neap and spring tide.

Four hundred mussels were laid out on the sand. Next day many had fixed their byssus onto each other and were lying in clusters together, but they had not been moved much. After 3 days they had been washed away considerably (fig. 9), and as time proceeded their distance from the original place increased and many could not be found again in the neighbourhood. After about 6 weeks all of them had disappeared. Strong westerly winds during July made regular inspection impossible, as the water did not sink far enough. The same applies to ε.

ε. This place was situated even lower than δ and was only exposed at extreme low water. The sequence of events was practically the same as at δ, but the mussels disappeared even quicker. After 3 days only 50 remained and when they were again inspected after 6 weeks they had all disappeared.

η. The current being apparently even stronger here the mussels were washed away in a very short time. Four hundred were laid out and the next day only 20 remained, 12 of which were

Fig. 10. η. Mussels remaining from 400 which had been put out 2 days previously. Only those which had a fixed point to attach themselves to have held out against the currents.

attached to the post. The others lay along the creek up to a distance of at least 100 m in SE direction. Two days later only the 12 on the post remained (fig. 10).

It is remarkable that at all the places the mussels were only washed along in the direction of the incoming tide, the flood current apparently being stronger than that of the ebb. We have already seen that this was apparent to some degree from the measurements of the current too.

To see how far mussels could be transported 400 mussels were painted with red lead and put down at η (fig. 7). Next day they had sunk down a little in the sand and were fixed in clusters onto each other. After 3 days 263 could be found again above low water mark, all of them along the creek in a southeasterly direction. Many of the others must have gone down the slope of the creek. Fifty were still on the original place, 196 between there and 250 m distance, and 17 beyond that. One was found near the stone dam at about 400 m from its original place. After 9 days 117 were found, none being nearer than 4 m from the original place. After 12 days only 21 remained visible, all at a considerable distance. After 7 weeks 3 were found at 250 m distance, spun together with mussels which certainly had no paint on them. It seems probable from this that mussels are being transported constantly over the sands. As these mussels were still alive the transport does not seem to harm them; they can attach themselves again if they can find a suitable substratum.

Apparently, then, currents, if strong enough, can transport the mussels or sweep them from their place, and this surely is the reason why the animals do not occur on the sands in places which have a high current figure.

We have seen, however, that high currents can be withstood on the dike, and it is probable from this that the substratum is as essential a factor as the current velocity. We shall therefore take this factor into account, the more so as no explanation has yet been given of the absence of mussels on the higher, soft parts of the flats, where the currents are weak.

2. SUBSTRATUM

The currents have a direct influence on the composition of the substratum. Bruce (1928), studying the intertidal zone, comments upon this question in some detail. The stronger the current the coarser the grain of the material which can be transported by it and also of the material which is left behind by the current. As the water proceeds inwards over the flats the velocity becomes more and more reduced, and gradually lighter material will be deposited so that the mud of the bottom will be softer. The weakest currents prevail in the high southwestern corner of the flats, where Leidam and Vangdam meet; here we also find the softest mud.

While discussing the currents several facts have already been mentioned, which indicate the great importance of the substratum for the mussel. The animal can resist much higher currents on the dam than on the flats and the experiments also suggest that a stronger substratum might make life on the outer flats possible. Apart from the difficulty of fixing themselves on the sand there might be the disadvantage of the moving sand, which could cover the animals up. A third point to be investigated is whether perhaps the substratum can be so soft as to make it impossible for the mussel to live on the higher parts of the flats.

a. Substratum as a fixing point for the mussel

To see what was the significance of the substratum as a point to fix the byssus the following experiments were made. Eternite plates, measuring 125 × 130 cm, were put down in several

Fig. 11. z. Mussels on the part cleared of *Zostera nana* and *Chaetomorpha linum*. A bunch of *Chaetomorpha* lies to the right. The black dots (upper left side) are *Littorina littorea* (L.).

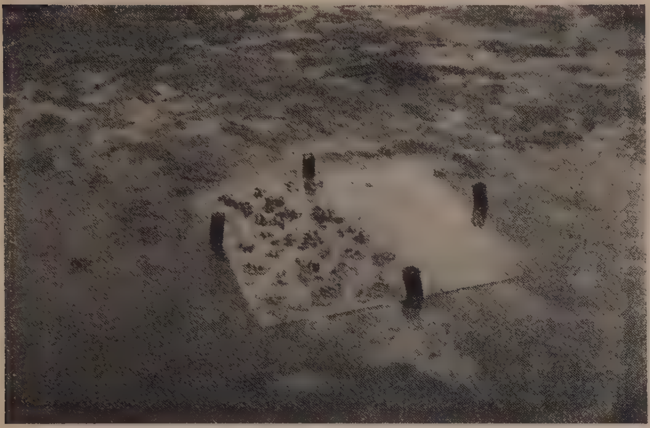

Fig. 12. *α*. Eternite plate with mussels put down on the left half. They have spun themselves together very nearly in the position in which they have been put out. The dark parts around them are mud which was left on their shells and has been washed off.

places, and mussels were laid out on these plates. Beside these plates mussels were laid out on the bare flat. The plates were fixed in position by four posts driven into the sand or mud. Half of each plate was covered with 400 mussels. Such experimental plots were laid out at *α*, *β*, and *γ*.

α. Very weak currents. Four hundred mussels were laid out amongst the *Zostera nana* vegetation, 400 on a similar area which had been freed from all covering plants, while 400 were laid out on the eternite plate.

In the mussels on the mud only few changes were observed. The mussels sank away a little or buried themselves until they were still about 1/3 above the surface. Most of them were spun together, but those which remained alone did not sink away either (fig. 11). Some were smothered by the sand which *Arenicola marina* L. constantly brings to the surface, but they were only few. After 2½ months 350 of them were still to be found in the area cleaned of vegetation. In the *Zostera*-covered area counting was more inaccurate, but only a few had disappeared.

The mussels on the eternite plate fixed themselves in a short time, mostly in groups of 5–15 together. After that no great changes could be observed (fig. 12). As there was practically no sedimentation here only very little material collected between them and little faeces were added to this (see p. 152).

β. Somewhat more current than at α. There was no vegetation of *Zostera* at this point. 400 mussels were laid out on the mud and 400 on an eternite plate. These last remained in position after they had fixed their byssus and were still present after 3 months. The fate of those on the mud was the same as at α. The activity of *Arenicola* was perhaps slightly greater, but had hardly any influence on the mussels.

In these places then, both α and β, there seems to be no great difference between what happens to the mussels on the plate and to those on the mud itself.

A much greater difference could be observed further out at γ.

γ. The 400 mussels put out on the flats were gradually washed away, as has already been described (see p. 130).

Beside these again 400 mussels were laid down on an eternite plate. These held out for a considerable time and after 3 months a few still remained. After the first tide they had all fixed themselves with byssus to the plate and to each other. All had been washed to one side of the plate, however (fig. 13). Probably this was because they had not fixed themselves when the first flood water came, whereas by the time the water was ebbing they had had time to fix themselves sufficiently. In the course of time great

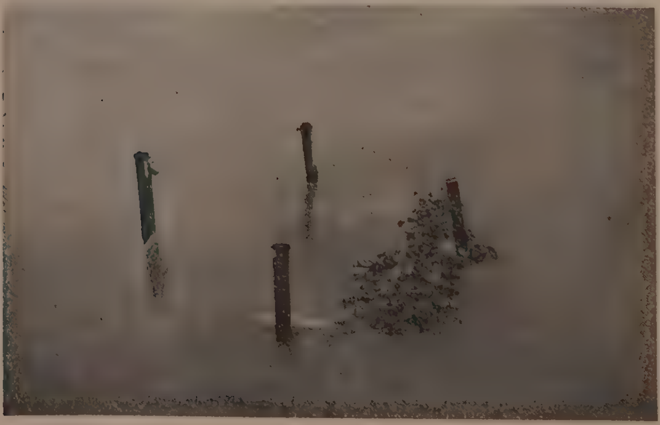

Fig. 13. γ. Mussels driven together by the current. They had been put out as shown for α in fig. 12. The plate has already partly been covered with sand.

quantities of material, which threatened to cover them up, were collected between the mussels. To save themselves they had to loosen their hold on the plate and had to climb higher. Thus, however, their hold grew less strong and gradually some of them were washed away. After two months there was 6 cm of sand in some places. After nearly 3 months 30 still remained, but 50 had been taken off previously for the determination of the quality index (see p. 151).

On the mussels here *Ulva lactuca* L. grew in large quantities, though higher up on the mussel beds no such growth was observed. Probably *Ulva* occurred here because the place was somewhat lower and *Ulva* cannot stand long exposure. Several authors mention *Ulva* as a passive enemy of the mussels, as it can smother them (FIELD, 1922; HAVINGA, 1929). Whether this was a factor of any influence in the disappearence of the mussels here could not be decided.

The fact must here again be mentioned that the posts which marked out the flats in squares of 200 × 200 m often had several mussels attached to them. This observation, together with the results of the experiments, shows clearly that the sand is insufficient support for the mussels and that the currents sweep them away. It seems to be due to this that no mussels occur here.

b. Covering with sand

The next point to be discussed is the influence of the sand which is constantly being transported over the flats and which might have some influence, as it may cover up the mussels.

We saw that the mussels on the outer parts of the flats, whether they were lying loose on the sand (η) or were fixed to some hard substratum (γ), were covered by sand, and we saw them trying to get out of it again (γ). It has often been mentioned covering with sand or mud is very injurious to the mussel. Thus, WRIGHT (1917) says that mussels always died in from four to five days when covered by sand, and that with even the slightest covering they made no effort whatever to raise themselves above it or otherwise to free themselves.

I made similar experiments and came to different conclusions.

Five mussels of 8 cm were put in a small aquarium with a thick layer of sand and running sea water, and covered by a layer of ½ cm sand. Next day 3 had worked themselves up so much that their siphons had appeared, while the fourth showed itself after 5 days. The last one had died in the mean time.

Covering the remaining four with 1–1½ cm of sand three reappeared within 4 days and the fourth after 5 days. Covered with 2 cm of sand none reappeared and after 6 days two had died. The other two died in the next 3 days.

Apparently some mussels can live for several days under the surface. How exactly they manage to work themselves up I could not see. At a certain moment they appear at the surface and then work themselves still higher up, but no movement was ever actually observed. The most probable explanation seems to be that they succeed in changing their position with their foot, raising the sipho, while the umbo was lowered. When the layer of sand covering them is too heavy they are not strong enough to change their position and die of suffocation.

c. Sinking down

Many authors have stressed the point that a soft substratum will not support the mussels and that they will sink away into it.

Among them Nienburg (1925) is of this opinion. According to him the occurrence of *Fucus* on mussel beds can be considered a symbiosis. The mussels would be kept at the surface by *Fucus*, while the *Fucus* would profit from the presence of the mussel, as it serves as a holdfast on the otherwise bare flats. Lehmann (1933) supports this hypothesis, but Thamdrup (1935) opposes it and thinks there is no question of such a symbiosis.

We have already seen that the mussels put out on the moderately soft parts of the flats (β), and even those on the very muddy parts (α), did not sink down. They were, of course, not supported by *Fucus* either.

To see whether it is possible for mussels to sink away in soft mud a few experiments were made in the laboratory. The experiment was made with ordinary mud from the flats, which was further treated as follows. An amount of mud was thoroughly mixed with sea water and then allowed to stand for 5 minutes, the coarser material thus sinking to the bottom. The water was then poured off into a bucket and left for 24 hours, after which period most of the suspended material had settled. This was put into an aquarium and used for the experiment. Water gently circulated over it so that it did not stir up the mud. Eleven mussels were put on this mud: four, about 4–4½ cm long, were put onto the mud in normal position (foot downward), two of the same size were stuck with the umbo downwards into the mud and two with the umbo upwards, these last four emerging about

1/3. Three mussels of about 1½ cm length were put down sideways.

After a few minutes the small ones put out their foot and started searching the surface for a holdfast. They crept about the surface and succeeded in remaining on top of the mud. Every now and then one would sink away a little, but they all worked themselves up again sooner or later. Next day all had reached a larger mussel and attached themselves to its shell.

The larger ones remained quiet for some time longer, but within 20 minutes they were all working with their foot, except those which were put in with the umbo downwards. These did not move, except that they opened their valves.

The two mussels with the umbo upwards had disappeared completely within 24 hours. It was obvious that they had searched with their foot for something solid, or tried to get hold on the surface of the mud with this organ, which was flattened out during these searchings. A good-sized *Cardium* shell was laid down beside one of them. It was immediately pulled down by the mussel as it tried to work itself up by it. Both mussels sank further and further until they touched the bottom of the aquarium and were then removed.

Of the four mussels which were put with their foot downwards three gradually disappeared into the mud as they crept about, probably searching for a hard object. Only one which lay quite still remained at the surface.

It appears from these observations that when the mud is extremely soft a mussel of some size cannot remain on the surface and will gradually sink away.

After some time, however, the material in the aquarium had consolidated and had become firm enough for the mussels not to sink. It follows from this that even the very finest material, which will probably never be found under normal circumstances, becomes firm enough to support the mussels, and NIENBURG's supposition that the mussel would need *Fucus* to support it on the soft mud apparently does not hold.

It was remarkable how small beds of *Mytilus*, especially far out on the flats, but also on the softer western parts, were often completely covered with *Fucus*. This alga might play a significant part in the life of the mussel, as it might help to hold the mussels together in strong currents or might act as a silt collector specially in view of the fact that large amounts of silt are being transported over the flats constantly (see below, p. 148). To see what

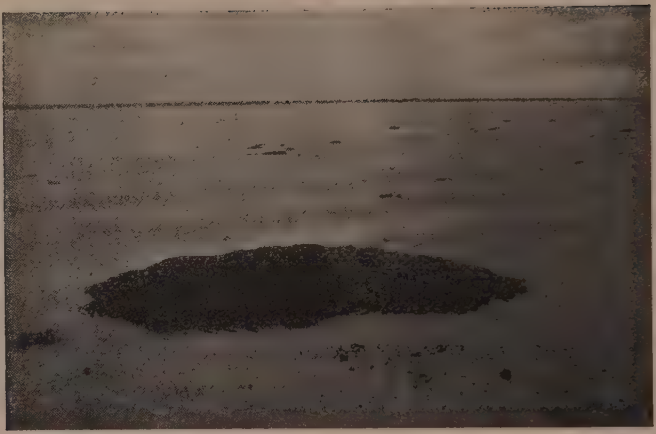

Fig. 14. A small bed which was originally completely covered with *Fucus spiralis*. Right part cleared. Position near M. B4 is visible in the background. Near the Malzwin C5 can be seen. The red stick which marked the middle of the bed can hardly be seen (Isochrom).

influence *Fucus* had the algae were removed from one half of a few beds, so that the mussels were freely exposed, while the other half of each bed was left in its normal state. Fig. 14 shows the appearance of one of those beds which had thus been cleared of algae.

Two places were taken on the sandy and one on the muddy part of the flats. Observations were made regularly. It soon appeared that where the currents were strong the material between the mussels was quickly washed away when *Fucus* was not present. The mussels first of all were freed from the surrounding silt, and then they soon started sinking lower. The sequence is shown diagrammatically in cross section in fig. 15 (see also fig. 16). In the two beds exposed to strong currents the process was a quick one, and after 5 days the mussels were already sinking down, while where the currents were weak it took about 3 weeks to reach this stage. After that the mussel beds in the strong currents gradually began to be swept away.

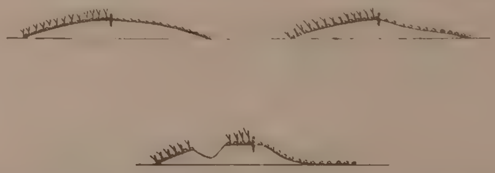

Fig. 15. Diagrammatic drawing of the sequence of events on the mussel bed which had partly been cleared of *Fucus*. The hole in the left side is not essential; it does not spoil the demonstration and incidently shows that the beds may be easily broken up by waves and currents.

It should be mentioned that where the currents were strong the mussels were much more firmly attached to the *Fucus* than where they were weak, and in the latter case the *Fucus* could be removed much more easily. *Fucus* may be of use to the mussel by forming a foothold against the currents, but the process is harmful to the alga, as the strands thus spun in by the mussels are soon covered up with mud.

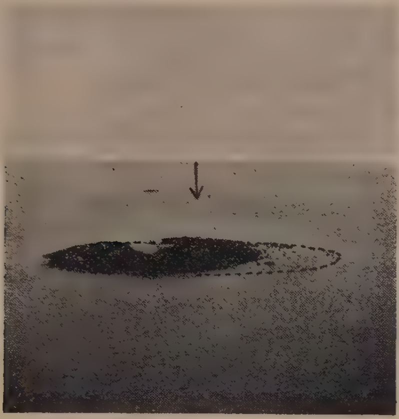

Fig. 16. Showing the same bed as fig. 14 after the right half had been cleared 2½ months previously. The dotted line delimits the original outline of the bed. The arrow points at the post marking the original centre of the bed. Left side broken up by waves, etc. B4 in the background. The water is not quite as low as in fig. 14, but even then not many more mussels would have shown above the surface.

From the observations and experiments so far described we may draw the following conclusions.

In those parts of the area studied where we find coarse sand and strong currents the mussel cannot resist these currents and is swept away by them. If a suitable substratum is present, which will not be covered by the sand (e.g. the concrete posts), the mussels can live very well there. Spun together with *Fucus* they can probably hold out longer, but these small beds never remain for any length of time.

On the soft substratum they do not sink down, and specimens remained at the surface for at least 3 months. We must look for some other reason for the absence of mussels here.

3. TIME OF EXPOSURE AND WEAK CURRENTS

In the first chapter the conclusion was reached that a low current figure was unfavourable to the mussel. This low figure resulted both from a long time of exposure and from the weak currents so that both the factors should be considered at the same time to see what influence either of them might have upon the mussel.

During the time the mussels are not covered with water they are exposed to the following influences:

a. desiccation,
b. extreme temperatures,
c. extreme salinities,
d. temporary oxygen deficit,
e. temporary food deficit.

The weak currents and nearly (or even entirely) stagnant water would expose the mussels to:

1. extreme temperatures,
2. little oxygen,
3. little food.

Desiccation and high salinity could only be due to the long time of exposure, not to weak currents, while extreme temperatures to a certain degree, and oxygen and food shortage even more, could be due to both factors.

We will now discuss these factors separately.

a. Desiccation

It is not probable that this factor would have a direct noxious influence on the mussels, as they close their shells firmly as soon as they emerge from the water. The factor is certainly subordinate to the oxygen shortage.

b. Extreme temperatures

The mussels high up on the flats are exposed to more extreme temperatures than those further down. The water which remains in the pools is heated by the sun, and a few measurements of the temperature near α showed that 28° C is by no means an uncommon temperature in the height of the summer. I omitted to measure the temperature of the mussels exposed freely to the rays of the sun, but on days with little wind the dark shells will certainly take up a great deal of warmth. Evaporation can help the animal little, as the shells are dry very soon, with not even a wet line where the two halves of the shell meet. As this point was not studied any closer the question of the high temperature remains an open one, and the possibility remains that high temperatures help to delimit the area where the mussels can be found.

As regards low temperatures we know that strong frosts may kill all or practically all mussels which are uncovered at low water. Severe cold in December 1938 killed nearly all the mussels in this area. Elsewhere the same has been observed after the hard winter of 1929 (BLEGVAD, 1929; CAULLERY, 1929). The only mussels which were found alive were those in between the stones of the dam and some of those which lived in the creeks on the flats. The first apparently profited from the warmth given off by the stones, while the last may have survived through their perpetual immersion. As nearly all the mussels in the intertidal zone were killed it does not seem possible that severe cold had any influence on the distribution there, though a less severe winter might kill the mussels higher up and not those lower down.

c. Extreme salinities

Though no salinity data are available the area studied is so small that there probably is no gradient of salinity in the water covering the flats during rising tide. As there is no direct draining from land onto this part the only source of fresh water is rain. Now, if a heavy shower were to fall during low water all the mussels on the flats would be exposed to it, but as they are closed during this time they would probably suffer no injurious effect. As soon as the water comes up they will open the shells. At that moment the sea water will be slightly diluted with the fresh water. The effect of this dilution will be the greater the higher we are on the flats. We must remember, however, that even a heavy shower will be of little influence as compared to the enormous quantities of sea water with which it is mixed. I think, therefore, that this factor can be of hardly any importance. All the same it seems to be of interest to make a further study of the salinities on these flats.

d. Want of oxygen

It has already been mentioned that the oxygen might be a limiting factor as a consequence of long exposure or weak currents. It must be added, however, that the thin layer of covering would be to the good, as it would make it more easy to resaturate the water with oxygen, should a deficiency occur through the slow currents, than a thick layer of water.

To get some insight in the oxygen requirements a few experiments were made in the laboratory. As we were particularly interested in the uptake of oxygen from more or less rapidly running water the experiments were made under circumstances which were rough imitations of natural conditions. Into a channel of 200 cm length, 10 cm width and 6.5 cm depth water from the aquarium of the laboratory was introduced. The flow of the water could be regulated, and its velocity was ± 8 m/min. at its maximum. Into this channel 147 mussels of about 6–8 cm length were brought, covering an area of 125 cm length and the total width of the channel. Determinations of the O_2-content of the water were made with WINKLER's method in bottles of about 250 cc contents with a correction for nitrite according to ALSTERBERG (see MAUCHA, 1932). Samples were taken before and after the water had passed over the mussels, and the values were compared. Only those values were used, where the duplicate determinations did not differ more than 0.03 cc/l. The amounts of oxygen used under these circumstances varied very much under the influence of largely unknown factors, but as a general conclusion we can say that the amount of oxygen used is very small. The initial oxygen content of the water was always 98–90% and the consumption at a current rate of $7\frac{1}{2}$–$8\frac{1}{2}$ m/min. was 0.04–0.10 cc/l or 0.7–1.8%.

For example: 13–VIII–36. 15^h00. T = 17°.8 C. S = 30.75. Current: $8\frac{1}{2}$ m/min. Water before mussels (w.b.m.) 5.48–5.48 cc/l; water after it had passed over the mussels (w.a.m.) 5.44–5.44 cc/l. Consumption **0.04** cc/l.—2–IX–36. 14^h45. T = 18°.4 C. S = 29.35. Current 8.5 m/min. W. b.m. 5.52–5.55 cc/l; w.a.m. 5.47–5.47 cc/l. Consumption **0.06** cc/l.—6–IX–36. 12^h40. T = 18°.3 C. S = ? Current $7\frac{1}{2}$ m/min. W.b.m. 5.34–5.35 cc/l; w.a.m. 5.23–5.26 cc/l. Consumption **0.10** cc/l.—13–IX–36. 10^h00. T = 17°.6 C. S = 30.43. Current $7\frac{1}{2}$ m/min. W.b.m. 5.48–5.49 cc/l; w.a.m. 5.40–5.40 cc/l. Consumption **0.08** cc/l.—Etc.

When large amounts of material had collected between the mussels (chiefly faeces and pseudofaeces) the consumption was somewhat greater (0.07, 0.10, 0.11, 0.15, etc.). When the current rate was reduced to $1\frac{1}{2}$ m/min. the consumption rose to 0.17–0.24 cc/l, which is 3.2–4.5%.

4–IX–36. $14^{h}45$. T = 18°.7 C. S = 29.35. Current 1½ m/min. W.b.m. 5.34–5.32 cc/l; w.a.m. 5.17–5.14 cc/l. Consumption **0.17** cc/l.—Idem $15^{h}15$. W.b.m. 5.38–5.34 cc/l; w.a.m. 5.13–5.17 cc/l. Consumption **0.21** cc/l.—Idem $19^{h}45$. W.b.m. 5.35–5.35 cc/l; w.a.m. 5.17–5.14 cc/l. Consumption **0.19** cc/l.—6–IX–36. $14^{h}55$. T = 18°.5 C. S = ? Current 1½ m/min. W.b.m. 5.19–5.17 cc/l; w.a.m. 4.93–4.94 cc/l. Consumption **0.24** cc/l.—Etc.

After a period of emergence, varying in these experiments from 12 to 26 hours, the amounts of oxygen consumed were 2 or even 3 times higher in the first hour. After that time, however, the rate of oxygen consumption was always reduced to the normal level.

4–IX–36. $9^{h}10$, after a period of emergence of 12 hours, the water is again made to flow over the animals. T = 18°.6. S = 29.35. Current 7½ m/min. $9^{h}20$. W.b.m. 5.46–5.44 cc/l; w.a.m. 5.19–5.25 cc/l. Consumption **0.23** cc/l. $9^{h}35$. W.b.m. 5.47–5.51 cc/l; w.a.m. 5.37–5.38 cc/l. Consumption **0.11** cc/l. $10^{h}10$. W.b.m. 5.48–5.50 cc/l; w.a.m. 5.42–5.40 cc/l. Consumption **0.08** cc/l. No further determination was made with the same current rate that morning. The last determination on the previous day (before the mussels were laid dry) gave a consumption of 0.07 cc/l; while the next determination with a current of 7½ m/min. (two days afterwards) gave 0.10 cc/l. We can therefore take the last value of 0.08 as normal.—7–IX–36. $9^{h}40$, after a period of emergence of 13 hours, the water is again let over the mussels. T = 18°.2. S = ? Current 7½ m/min. $9^{h}47$. W.b.m. 5.25–5.23 cc/l; w.a.m. 5.08–5.12 cc/l. Consumption **0.14** cc/l. $10^{h}00$. W.b.m. 5.29–5.30 cc/l; w.a.m. 5.13–5.16 cc/l. Consumption **0.15** cc/l. $10^{h}35$. W.b.m. 5.23–5.26 cc/l; w.a.m. 5.20–5.20 cc/l. Consumption **0.04** cc/l.—10–IX–36. $17^{h}10$, after a period of emergence of 26 hours, the water is let over the mussels. T = 17°.6 C. S = 30.43. Current 7½ m/min. $17^{h}20$. W.b.m. 5.36–5.39 cc/l; w.a.m. 5.31–5.30 cc/l. Consumption **0.07** cc/l. $17^{h}35$. W.b.m. 5.36–5.35 cc/l; w.a.m. 5.31–5.33 cc/l. Consumption **0.03** cc/l. $18^{h}10$. W.b.m. 5.41–5.42 cc/l; w.a.m. 5.37–5.37 cc/l. Consumption **0.04** cc/l.—Etc.

There appears to be no direct relation between the period of emergence and the amount of oxygen taken up immediately after it. Moreover, the highest values are not always found immediately after the water has again covered the animals. This may be due to the fact that the mussels do not all open their shells at the same time, and it was frequently observed that only some of the animals were open and apparently active. This opening and closing of the shells was certainly one of the reasons why the results of these experiments were not more constant, and it may also explain the instance of a slight increase after a long time of emergence, as a gradual opening of the animals, one by one, would nullify the expected result.

Koller (1930, p. 442) observes the same inconstancy and he remarks on *Mytilus:* “Die Miesmuschel ist an Aufenthaltsorte mit stark wechselndem Wasserstand angepasst. Infolgedessen tritt bei ihr – oft scheinbar unvermittelt – völliger Schalenschluss und damit Aufhören der Sauerstoffaufnahme aus dem umgebenden Seewasser ein." DODGSON (1928, p. 194) mentions the same: ". . . mussels are prone to behave capriciously . . ."

The water on the highest parts of the flats was shown in August 1937 to be saturated or even oversaturated (105%) during daytime. This high value is undoubtedly due to the assimilation of the countless green organisms covering the whole surface of the muddy parts. We may assume that at night there is sometimes undersaturation (see BROEKHUYSEN, 1935), but I have no further data as to the amounts of oxygen on these flats at my disposal.

Mussels over a length of 125 cm are able to lower the oxygen content of the water, when its depth is 6.5 cm, by 3.2–4.5% when the current rate is 1.5 m/min. Thus, if the water flowed over a mussel bed of 12.5 m at this rate the oxygen content would be lowered by 30–45%. We can, therefore, imagine that water flowing during the night over the mussel beds and the flats with the thousands of other organisms would become quite undersaturated if the rate of the water was slow.

There are, however, several reasons for thinking that low oxygen tensions are less harmful to the mussels than these considerations would at first lead us to suspect. First of all, the lower the oxygen tension the more oxygen the water will take up from the atmosphere. Secondly, as already stated, the shallow layer of water is easily resaturated from the atmosphere. Thirdly, the experiments seem to prove that mussels, even after long periods of exposure to the air, very soon catch up with their normal consumption of oxygen. If long exposure would cause serious oxygen shortage in the animals they would have ample time to regain their normal consumption even if the time of submergence was only a few hours during each tide. On the other hand, during neap tides and easterly winds, the water may not reach the upper parts of the flats or only cover them insufficiently and it is not impossible that the mussels very high up would suffer from serious want of oxygen then.

Further investigations, which will be discussed in detail below, showed that the mussels declined rapidly in condition after they had been living on the high parts of the flats for 2–3 months in the summer (July, August, September 1937). It was in this period certainly improbable that the oxygen content of the water would be too low and that the oxygen supply would have been insufficient for the animals. HAZELHOFF (1938) has recently shown that those animals which use the same mechanism (viz. a water current produced by a ciliar movement) both for feeding and respiration must maintain a much stronger current to obtain sufficient food than would be necessary to satisfy their oxygen want. In other words, they show a very small consumption of oxygen per unit volume of water passed along the gills. It is therefore improbable that such animals as the mussel would get short of oxygen and it is much more likely that the amount of food in weak currents is insufficient.

This will now be gone into in some detail.

e. Want of food

We have seen that none of the factors which have been discussed up to now gave a satisfactory explanation of the upper limit of the mussels on the area studied, and that, indeed, food might be most significant of all.

The question what kind of food is the chief or only source of energy for the mussel has not been solved definitely.

BLEGVAD (1914) thought that detritus was the principal food. His conclusions are based on the observations of the stomach contents of 157 mussels, which were collected from 37 different localities. In all these cases he was convinced that detritus was not only the main part of the stomach content, but also that it served as food. FIELD (1922) considers plancton of importance too, while HAVINGA (1929) draws attention to the possibility that bottom organisms whorled up by the currents might form a considerable food supply. He stresses the point that different conditions may prevail in different localities, and that this might account for the difference in opinion. FOX (FOX et al., 1936) finds that phytoplancton is the main source of food for *Mytilus californianus*, but this animal lives under different conditions to *Mytilus edulis*, and the results of his investigations can therefore not be applied directly to the latter. FISCHER (1929) is convinced that dissolved organic matter is the main food source for the mussel and thinks that the distribution in a certain area which he studied can be explained by this assumption. He fails, however, to prove his assumption, and his explanation of the distribution is just as good even without drawing this very questionable supposition of dissolved organic material as food into the discussion.

Whatever the final answer, we can be sure that the food has to be brought to the mussel by the currents. The animals are, therefore, dependent both on the amount of food per unit of water and upon the current velocity. HAVINGA (1929) formulates it thus: For good growth current × food content must have a certain value. As KREGER (1940, p. 193) already pointed out, increase of current velocity above a certain value has no further influence on the food supply, because increase only has any effect if food can still be taken from the water more quickly than the currents bring it along.

In the area we have in consideration the amount of food per volume unit of water is to a certain degree dependent upon the current velocity, as more material is suspended in stronger currents. The amount of food per volume unit of water cannot be determined, as we do not know what is actually taken up as food. We can, however, take some value in approximate correlation with the amount of food in order to get an idea of the amount at the disposal of the animals. As such the organic part of the material suspended in the water was taken. Certainly the amount actually used as food is less, but the amount in different places will be sufficiently proportional to that value to allow us to use it for comparison. If we can estimate the amount of material which is transported at a certain place, and determine the percentage of organic material, multiplication will give us a value for the organic matter at the disposal of the animals, which can be compared to that at other places.

The amounts of material transported over the flats has to be determined first. The best way to do this seemed to be to put out jars, which were dug into the sand in a vertical position, and to compare the amounts of material collected in them. Though there are certainly objections to this method, as it is not really quantitative (MARSHALL & ORR, 1931), the values can be used very well here as we are specially interested in the relative values for the different parts of the flats. The possible influence of different weather conditions was not taken into account.

The jars used were 21 cm high, the opening was 31 cm^2, while the inside diameter was 7.9 cm. They were buried exactly vertically in the sand, leaving the top 3 cm above the surface; the jars placed in the mussel beds then had the top level with the mussels. Jars were put out in the following points (see map): γ, B3, M, just SW. of M, A3, p, and α.

The amount of material collected varied considerably at different times, but it is obvious that, as we go further out on the flats towards the open sea, the amount of transported material increases greatly (see table 2).

TABLE 2

Amounts of material collected in the jars on the flats in cubic centimeters

	21–26, VII.	23–26, IX.	13–26, IX.	1–3, X.	13, IX–3, X.	per day
α.	–	–	–	–	a:265*) b:196	10–13
p.	–	–	430	84	–	33–42
A3.	–	59	–	69	–	20–34
20 m SW of M.	450	–	–	122	–	90–61
M.	615	620	–	412	–	123–207–206
B3.	860	196	–	343	–	172– 65–171
γ.	–	570	–	760	–	190–380

*) *a* = normal *Zostera* vegetation.
b = *Zostera* cleared away.

The only discrepancy lies in the mussel beds themselves, which collect large amounts of suspended matter during the whole time of covering, partly as food, partly because any rough surface will collect material. Most of the food is reproduced in the form of faeces or pseudofaeces, which, being comparatively heavy, will sink down sooner than the original material would have done. Therefore, while in other places the finest suspended material will only sink down when the current becomes very

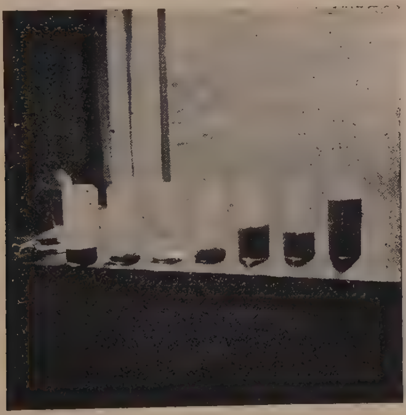

Fig. 17. Amount of material collected in the jars put out on the flats. The jars were taken from the positions mentioned in Table 2 (p. 149); α is on the left, γ on the right side of the photograph. The jar from α had been out 20 days, all the others 2 days.

weak, here great amounts will be collected while the currents are still much stronger, and the amount of material collected in the jars will consequently be very much larger. Fig. 17 shows the results of the experiments from 1–3 X 1937 for the localities p–γ and a jar from α which had been put out from 13 IX–3 X 1937. The differences are obvious.

The quantities of material collected in the *Zostera* field are very low, which fits well with the observation that the sedimentation at α on the eternite plate was practically 0. When the incoming tide was observed there it was seen that the water, which was dirty as it came over the flats, was cleared within a few meters as soon as it came to pass through the *Zostera*. Probably there is some sedimentation in the outer parts of the *Zostera* field.

Having thus gained some idea of the relative amounts of material transported over the flats the next point was to determine the amount of organic material it contains. To this end it was assumed that the loss on ignition is chiefly due to organic material (MARSHALL & ORR, l.c.). The method is not very accurate, as there are several sources of error, such as crystallisation water and the decomposition of inorganic salts, but only relative figures were needed and the conclusions can therefore be considered valid.

TABLE 3

Organic material in the jars in percentages

α.	± 14
p.	6.5– 6.6
A3.	3.9– 3.9
M.	14.9–16.4
B3.	10.1–10.7
γ.	4.1– 4.0

A determination was made in the following way. A small amount of material, about 15 g, was weighed and dried for two hours at 120° C, and then weighed again. Taking the amount of salt per gram of evaporated water to be 0.033 g the amount of salt in the dry weight and therefore also the dry weight of the material minus the salt were known. The material was then heated on an open Bunsen flame for 1½ to 2 hours, having been ground in a mortar beforehand. Both after the drying and after ignition the material was allowed to cool for half an hour in an exsiccator, and finally weighed again. All determinations were made in duplicate. The results of one such series are given above.

The high values for M and for B3 are undoubtedly due to the great amount of mussel faeces, which not only sink down on the mussel beds themselves, but also at a small distance from them.

If we compare α and γ, where there is no influence of the mussel beds, it is obvious that the amount of organic material is much larger at α. On the other hand, the amount of material transported there is much smaller. To get a measure for the quantity of food the mussels can obtain we had to multiply the quantity of transported material and its percentage of organic matter. For the quantities we have relative figures only (table 2), and we can thus calculate only relative amounts for α and γ. These are 161 for α and 1140 for γ. As this is only a rough method all we can say is that the amounts compare as 1 : 7. This would seem a very good reason why no mussels are found in the neighbourhood of α.

Dodgson (l.c., p. 191) mentions that mussels did not open when the water was stagnant, but opened as soon as a current was set up. Though this is certainly not a rule (in fact, I never observed it myself) it may in the long run have some influence, and would be a further reason for the mussels not being able to live on the higher parts of the flats.

The mussels which were put out on the higher parts in the beginning of July were still alive in September, but it was possible that their condition had become worse. To get certainty on this point the quantity of their flesh was determined by a method introduced by Havinga (1922, p. 377), and the figure compared with that of mussels which had been left in their original place.

Havinga, being interested in the amount of flesh per unity of total volume inside the shell, should have determined the dry weight of the flesh and the weight of the shell contents, water included. For practical reasons he made use of other figures: the total weight of the living animal, the dry weight of the shell, and the weight of the flesh after 7 minutes boiling. By subtracting the weight of the shell from the total weight and dividing the weight of boiled flesh (instead of the dry weight) by this value, he got a measure for the water content of the animal. Havinga named the figure thus obtained the quality index.

I determined the quality index as follows. Each mussel was taken from the water carefully and touched lightly so that it closed the shells gently. It was then dried with a cloth, weighed, and put in boiling water (tapwater) for 7 minutes. The animal could then be easily removed from the shell, and was dried between filterpaper and pressed gently to get the water from between the contracted gills. It was then weighed again, the shell weight being determined also.

Havinga found the lowest value in the former Zuiderzee, viz. a quality index of 0.125, the highest in the Waddenzee near the island Griend, with 0.45 as quality index.

The quality index of the mussels from the Zuidwal appeared to be very low. The mean for 50 mussels from M was 0.221 ± 0.0069 [1]). Apparently the circumstances were not very good. Those which had been at γ for two months had as a mean 0.229 ± 0.0069 (for 60 animals), so that they did not differ significantly from those from M, where they had been taken. For the mussels from α, however, the mean after two months was 0.138 ± 0.0042 (for 60 animals). Their condition was apparently very bad and the animals were on the verge of starvation.

It would, besides, have been interesting to make accurate quantitative determinations of the stomach contents. These were not made, but the following data show that there was a remarkable difference between the mussels from M and from α. The amounts of faeces + stomach contents were determined by putting them in filtered water after they had been cleaned thoroughly from the outside. They were left in this water until they produced no more faeces. It was not possible to separate the real faeces and the pseudofaeces from each other, but the difference between the two batches of mussels was so obvious that this did not seem to be necessary. Mussels from the natural beds produced at least 4–5 times as much as those which were taken from α. In addition to this it was found that newly collected mussels from M often had some food in their stomach, while the mussels from α were always completely empty.

We have thus found that the quantity of material suspended in the water at α is very low, and though the percentage of organic material is relatively high, the total amount of organic material is about one seventh of that farther out on the flats. We have further seen that the quality index of the mussels which had been at α for two months was very low as compared with those at M, where they were taken from. The mussels at α

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[1]) The mean square error, calculated with the formula $S = \sqrt{\frac{\Sigma \delta^2}{n(n-1)}}$

further had empty stomachs and gave off very small quantities of faeces and pseudofaeces. From all these data I think it may be concluded that the mussels on the higher part of the flats have insufficient food at their disposal, and that this is the reason why they do not occur there normally. This lack of food will probably be principally due to the weak currents, but it is impossible to say how much of it is due to the short duration of covering.

CONCLUSION

We should now try to form a picture of the conditions on the flats and see whether we can explain the distribution of the mussels by what we now know of the factors which influence them.

The distribution itself has the following characteristic points. The mussels occur in great abundance on the dike and on the posts on the sandy parts of the flats. Besides, on the flats themselves they chiefly occur in a long narrow strip, which lies at an approximately uniform level. Above this level we find the softer part of the flats, while below the bottom is hard and sandy.

Current measurements showed that mussels occur at a certain medium value of current figure, which expresses both the strength of the current and the period the currents run over a certain place. Experiments made it clear that the high velocity of the currents, which is associated with a high mean current figure, is the factor which makes life impossible on the outer parts of the flats. The currents sweep them away, unless they find a good substratum to fix themselves. Such a substratum is formed by the concrete posts and the stone dam.

The reason why the mussels do not live on the higher parts of the sands is somewhat less simple to analyse. It is obvious that both weak currents and long exposure create unfavourable conditions, the softness of the substratum, associated with weak currents, being of little influence in this respect.

The deleterious influence of weak currents and long exposure probably is a combined one, involving several factors, but one of these seems to be by far the most important: the factor food.

Desiccation, temperature and salinity may have some influence, but their significance is certainly less than that of food. Determination of the oxygen consumption of mussels in flowing water, together with observations on the flats, do not make it probable that want of oxygen can be of much influence in governing the limit of distribution towards the higher parts of the sands either.

Food supply, however, is of prime importance. Determination of the amount of organic material suspended in the water showed that it was small in the higher and great in the lower parts of the flats (although the percentage of organic matter in the suspended material was much higher in the highest parts of the flats). Moreover, the small amount of faeces produced by the mussels from the higher parts and the empty stomachs of these animals showed their starving condition. There can be little doubt, therefore, that want of sufficient food is the most important limiting factor on the higher part.

It was stated in the description of the flats that a sharp demarcation line marks the northeastern boundary of the mussel beds, whereas to the southwest the beds grow gradually smaller and a sharp line is absent. I think that the fact that mussels do not, as a rule, occur singly, but generally in beds, is an essential point to be considered in trying to explain this obvious difference. The mussels fix themselves onto each other and in a body can stand the higher current better than alone. To the northeast of the beds, where the currents are strong, they will therefore either hold in a body or be all swept away; a gradual falling off in numbers would therefore be impossible. To the southwest of the beds, however, where there are no strong currents and the distribution is limited principally by a factor (or factors) associated with long periods of emergence and weak currents, this formation of beds has no influence and indeed we find a much more gradual decrease of the numbers as the severity of the conditions increases.

The results are of interest not only for the distribution of the mussels on the flats in question, but also in connection with the distribution of mussels on other intertidal sandflats or even in the intertidal zone generally. The observations show that mussels cannot form beds on the intertidal flats when the currents are strong, unless there is a firm base. It follows from the investigations of Wrage (1930, p. 95) and Kreger (1940, p. 184 and 189) that a firm base on the flats is regularly furnished by dense patches of cockles. The reason why such extensive areas of the intertidal flats are devoid of mussels or at least of mussel beds is probably partly to be sought in the absence of such cockle patches in these areas. The observations further show that the reason why the higher part of the intertidal zone generally is hardly inhabited by mussels is to be found in the shortage of suitable food.

SUMMARY

1. On a small intertidal sandflat area the distribution of *Mytilus edulis* is considered in detail. A description of the area and its mussel population is given.

2. Dispersal of the larvae or distribution of enemies cannot explain this distribution of the mussel. General observations made it probable that the currents are of extreme importance.

3. Currents were measured at different places every 15 minutes throughout a whole period of covering. A mean is calculated, and for each place a certain value for this "current figure" can be given. It is dependent both on the strength and the duration of the currents and on the period of submersion.

4. The results show that when the current figure is below a certain limit no mussels occur, and also that at a high current figure no mussels are found on the bare flats.

5. By putting out mussels on the sandy parts of the flats, where the currents are strong, it was shown that they are swept away by the currents. Painted mussels were shown to be transported over at least 400 m and some were still alive after one and a half months.

6. Comparing mussels on eternite plates and on the bare sand showed that they can live quite well on these sandy parts if they find a suitable substratum.

7. Experiments in the laboratory showed that mussels may sometimes be covered up for six days by a layer of sand without harm. If the layer of sand is less than 2 cm they may succeed in working themselves out. Covering up of the mussels by sand is, therefore, no important factor in limiting their distribution in the area studied.

8. The general conclusion from these observations and experiments is that the mussels do not occur on the sandy parts of the flat, because there is no proper place for them to fix their byssus.

9. In the laboratory it was shown that very soft mud furnished insufficient support for larger mussels, but after it had stood for some time it became firm enough. The substratum alone

cannot be the reason why the mussel does not live on the softer parts of the flats.

10. From the low current figure it can only be concluded that either the long exposure or the weak currents create conditions unfavourable for the mussels. The absence of mussels may be either due to desiccation, extreme temperatures (both the result of long exposure) or to extreme salinities, want of oxygen or want of food (the result of either long exposure or weak currents).

11. It is argued that neither desiccation or extreme temperatures, nor extreme salinities can be sufficient reason for the mussels not to occur on the higher parts of the flats.

12. In experiments with running water it was shown that the amount of O_2 used by the mussel is not very great. In summer and by day the amount of oxygen in the water on the flats is very high. Moreover, after a period of emergence, the mussels soon catch up with their normal oxygen consumption, within one hour at the utmost. This makes it improbable that oxygen should be the limiting factor.

13. The mussels laid down on the high parts of the flats were in very bad condition after two and a half months, as shown by the determination of the quality index according to HAVINGA.

14. The relative amount of food at the disposal of the animals was estimated by taking the amounts of organic material suspended in the water to be proportional to it. The amount of material suspended in the water was indirectly measured by putting out glass jars on the flats. The amounts collected in these were very small on the higher and very large on the lower parts of the flats. Although the percentage of organic material, determined as loss on ignition, was larger in the higher parts of the flats the relative total amounts were about 7 times as great in the strong currents as in the high corner of the flats, where only very weak currents prevail.

15. The mussels transplanted to a place high on the flats after some time produced very little faeces and never had anything in their stomachs.

16. From these facts and from what is known about the food supply it is concluded that the chief reason why mussels do not occur in the high parts of the flats is lack of food. Other factors may help to kill off such animals as have been able to stand this strain the longest.

17. The results are of interest in connection with the distribution of *Mytilus* on intertidal sandflats and even in the intertidal zone generally. Mussels cannot form beds on the intertidal flats when the currents are strong, unless there is a firm base. The higher part of the intertidal zone generally is hardly inhabited by mussels, chiefly because of the shortage of food.

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APPENDIX

After the manuscript of this paper had been finished the Zoological Station came into possession of an aerial photograph of the area studied. Moreover, in 1938, height measurements were made, thanks to the kind collaboration of Prof. Ir. W. SCHERMERHORN, by geodetical students of the Technical University of Delft. On the accompanying map (fig. 18) the results of these measurements are given relative to the Dutch datum level, Nauwkeurigheids Amsterdamsch Peil. The contour lines were drawn according to these measurements and observations made in loco and in accordance with the aerial photograph. As the points of measurements lie at considerable distance from each other only the contour lines with an interval of 25 cm could be drawn. Many details, therefore, do not appear in this map as, for instance, the creek running through the mussel beds near post A3. All the same, through these data the morphology of the flats has become much clearer. In the principle points there is no difference from the general description of the flats as given on p. 118. In one respect, however, the new data are of great significance for the problem under discussion. There is a distinct ribbing of the flats, which is seen most clearly in the photograph. This ribbing extends approximately between the posts B4 and B8 and the Vangdam, the direction of the ridges and

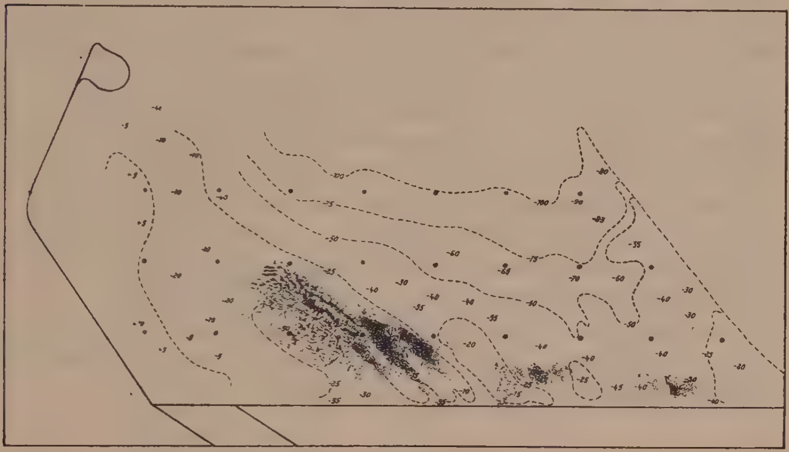

Fig. 18.

channels being about NNW–SSE. How it originates I do not know. It is certain, however, although this was not noticed during the investigations, that it has a marked influence on the distribution of the mussels. Part of what is black in the map may not be mussel beds, but all the same it is clear that the mussel beds occur chiefly in the low channels between the ridges and that they are more or less absent on the ridges themselves.

I do not know whether the correlation between the occurrence of the mussels and the morphological structure of the flats existed in 1935–'37 also. It should be remarked that the distribution of the mussels on the aerial photograph of 1938 (fig. 18) is different from the distribution on my own map (fig. 1), a fact confirmed by observations in 1939. It seems very probable, however, that this correlation existed in 1935–'37 as well.

Though an explanation cannot be given off hand the preference for the lower parts is apparent. Probably one of the factors which has been discussed in this paper plays some part here, but this can only be made out by closer investigation.

I can therefore do no more than draw attention to the fact that the contents of this paper only apply to the distribution in general and not to minor peculiarities.

ON THE HEART AND ARTERIAL ARCHES OF SALAMANDRA MACULOSA LAUR. AND AMBYSTOMA MEXICANUM SHAW DURING METAMORPHOSIS

BY

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I. INTRODUCTION

This investigation deals with the changes in position and structure of the heart and arterial arches of *Salamandra maculosa* Laur. (*S. salamandra* L.) during metamorphosis.

Publications on the changes in the heart and the arterial arches in larvae of Urodela during metamorphosis have only sparsely appeared.

Boas (1882) in his excellent work: "Über den Conus arteriosus und die Arterienbogen der Amphibien" describes the changes in the structure of the arterial arches during the metamorphosis of four consecutive larval stages of *Salamandra*. 1)

Changes of these arterial arches in urodelan larvae have of late been described by McMullen (1938) for *Desmognathus fuscus*, *Plethodon cinereus*, *Eurycea bislineata* and *Gyrinophilus porphyriticus*.

Langer (1894) studied the development of the bulbus cordis in two larvae of *Salamandra maculosa* (2.3 and 2.9 cm).

Greil (1903 A and B) examined the truncus in larvae of *Salamandra atra* from 6 mm onwards.

Hochstetter (1906) describes the development of the larval heart of *Salamandra atra* and gives reconstruction figures of larvae from 5.5–13 mm.

As far as we know, the larval heart of Urodela was last examined by Benninghoff (1922) especially in *Triton alpestris*. His investigations are mostly concerned with the origin of the auriculo-ventricular valves and the structure of the ventricular musculature.

The heart of adult Urodela is better known (cf. Körner, 1938, who describes the hearts of thirty-three species).

The heart of the adult *Salamandra maculosa* especially has of late been described by Züllich (1930), Francis (*S. salamandra* L.; 1934) and Körner (1938).

About the arterial arches of adult *Salamandra* we find important data in Boas (1882), Bethge (*S. maculata;* 1898), Königstein (*S. maculata;* 1903) and Francis (*S. salamandra* L.; 1934).

In connection with the remarkable development of this

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1) Where names of species or names of authors behind the specific name are omitted in the publications quoted, they have not been expressly stated by us in this paper.

animal the investigation was extended to *Ambystoma mexicanum* Shaw [1]) and after the descriptions concerning *Salamandra maculosa* Laur. the differences with *Ambystoma mexicanum* Shaw will be described.

Vague data relative to the heart of the axolotl are found in Calori (1851), Wyman (1854/56), Fritsch (1869) and Boas (1883).

Körner (1938) gives more accurate and extensive data on the adult heart.

Calori (1851) and Boas (1882) also give data about the arterial arches of these animals.

In this survey of literature we also want to mention the hardly scientific publication by Gilmore and Figge (1929) on the heart and aortic arches of *Ambystoma tigrinum*, which animal is apparently regarded as identical with *Ambystoma mexicanum* Shaw by these authors.

II. MATERIAL - TECHNIQUE

The material of *Salamandra maculosa* Laur. for this investigation consisted of one batch of seventeen larvae grown by ourselves from parents obtained from Messrs. Scholze & Pötzschke's of Berlin.

The animals were fed on Enchytraeid worms and killed in several stages of the metamorphosis by adding chloroform to a little water into which the animal was brought.

One or two days before they were killed the animals were placed in surroundings free from sand in order to prevent the presence of sand in the alimentary tract when sectioning the material.

Francis (1934, p. 7) has the following remark about the metamorphosis: "They grow slowly and attain a length of 55–65 mm in about 3–5 months, when they metamorphose and leave the water. The chief external changes noticeable just prior to metamorphosis are the appearance of yellow pigment, the approach to adult coloration, and the dwindling of the external gills. The loss of the swimming membrane on the tail follows immediately, and the head assumes the adult shape through the advent of the paratoid glands".

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[1]) For systematics and nomenclature of the axolotl see Wolterstorff (1930).

After these external characteristics the larval stages were arranged as accurately as possible. In table I these larvae have been arranged in the order of the stage of the metamorphosis. In this table are also stated their age, length of body and length of tail.

TABLE I

Number of animal	Age in days	Length of body in mm	Length of tail in mm	Stage of metamorphosis at the time of killing
1	1	23	11	
2	17	34	17	
3	33	36	18	
4	56	43	21	yellow pigment appearing slightly; tail and gills do not show any dwindling
5	74	47	23	yellow pigment not yet definitely shaped; swimming membrane shows some dwindling; gills dwindling very little
6	109	57	28	dwindling of swimming membrane clearer; gills dwindling strongly; pigment spots clearly present, however, not outlined
7	125	60	26	shape of yellow pigment makes itself apparent; only rest of the swimming membrane present; gills still present, very much reduced
8	102	61	26	wholly pigmented, however, not definitely shaped everywhere; tail very flat; only slight rest of swimming membrane; gills dwindling to stumps
9	109	60.5	25	idem

Number of animal	Age in days	Length of body in mm	Length of tail in mm	Stage of metamorphosis at the time of killing
10	102	54	25	no swimming membrane; tail flattened; slits not yet closed; short stumps of gills; wholly pigmented spots, rather clearly shaped
11	102	51	22	idem
12	127	65	22.5	pigment definitely shaped; slits nearly closed; gill-stumps reduced to rests; tail flattened
13	124	57	21.5	idem
14	102	50.5	22	tail less flat; slits closed; pigment definitely shaped; gill-stumps disappeared
15	102	51	22	all larval characteristics disappeared
16	120	54	19	idem
17	127	49	19	idem

The first symptom of metamorphosis – the appearance of yellow pigment spots – showed itself in one of the larvae (no 4) after 56 days already. The appearing pigment spots have at first very vague outlines and, in specimens of about ninety days only they are distinctly shaped.

The first signs of the dwindling of the gills was seen in a larva of seventy-four days old, while at that time the swimming membrane too shows dwindling already (no 5).

In some larvae (nos 14 and 15) the symptoms of metamorphosis follow each other very quickly, so that after one hundred and two days already they had lost all larval characteristics.

In other larvae the whole process of metamorphosis lasted for a considerably longer time (nos 7, 12, and 13). As appears from figure 1, there is some relation between the age and the length of body.

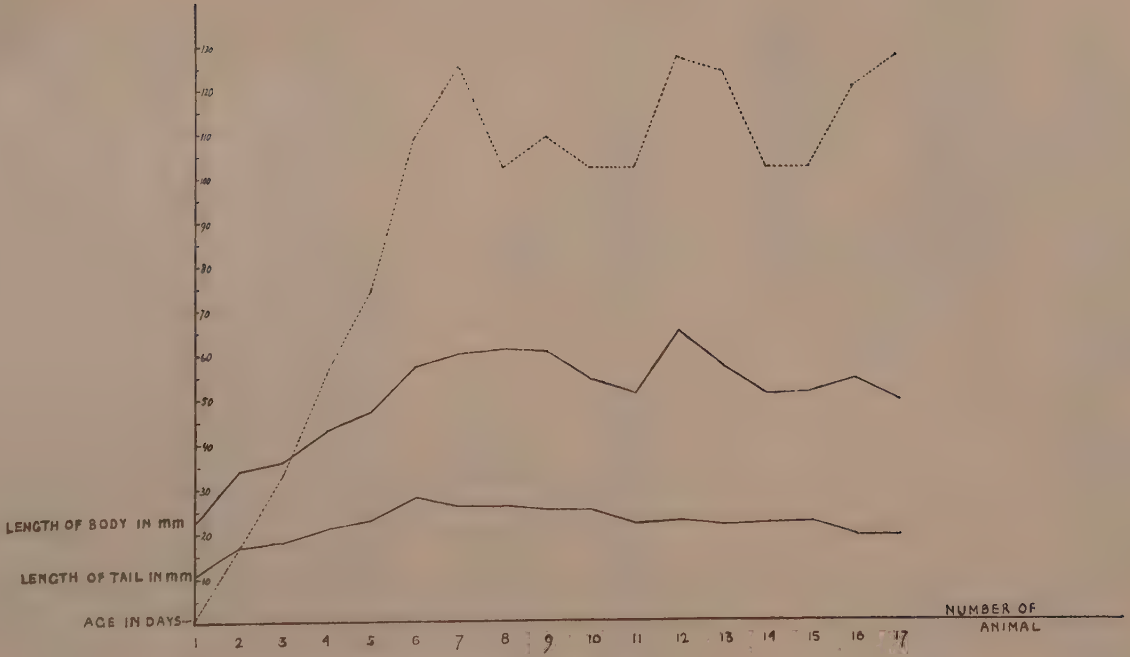

Fig. 1. Graphic representations of the age, length of body and length of tail.

One has the impression that during metamorphosis no longitudinal growth takes place.

However, during metamorphosis a direct relation between the age or the length of body and the stage of metamorphosis reached cannot be shown (fig. 1).

It is, however, evident that, when comparing the various stages of metamorphosis – especially where this comparison depends on internal dimensions, as size of the parts of the heart, diameter of the bloodvessels, etc. – we shall have to take into account the length of the body in the stages compared.

For this investigation a segment of the body–situated between the front of the gills and the middle of the trunk–was cut out and fixed by means of alcohol of 96%.

All this material was imbedded in paraffin and sectioned in transverse sections of 10 micra.

The serial sections were all stained with Mallory's connective tissue staining. [1])

For purposes of comparison with these stages of development, but also in connection with the description of the adult heart in literature, also a few adult specimens of the same species, obtained from SCHOLZE & PÖTZSCHKE's, were examined.

Of two adult salamanders the heart in the pericardium was prepared separately, sectioned in paraffin and stained with Mallory's connective tissue staining.

Of three adult salamanders a segment of the body lying between the back of the skull and the middle of the trunk, was cut out and fixed in alcohol of 96%. In connection with the sizes of these objects, as well as in connection with a thorough investigation into the structure of the septum atriorum, these animals were imbedded in celloidin, and stained with haematoxylin-eosin.

In table II a survey of these animals is given.

The celloidin series fell out rather badly, and are only exceptionally used for the investigation.

For purposes of comparison with the stages of development of *Salamandra maculosa* Laur. a number of larval specimens, besides

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[1]) See ROMEIS, P., 1932. Taschenbuch der mikroskopischen Technik. 13. Aufl., p. 414.

TABLE II

Number of animal	Length of body in mm	Object	Fixative	Medium of imbedding	Staining	Direction	Thickness in micra
18	145	heart	alc. 96%	paraffin	Mallory	transverse	15
19	140	heart	alc. 96%	paraffin	Mallory	transverse	15
20	150	segment	alc. 96%	celloidin	haematoxylin-eosin	transverse	20&30
21	146	segment	alc. 96%	celloidin	haematoxylin-eosin	transverse	25
22	135	segment	alc. 96%	celloidin	haematoxylin-eosin	transverse	20

some specimens artificially transformed, of *Ambystoma mexicanum* Shaw were examined.

Some larger axolotls (nos 29, 30 and 34) were preserved in alcohol, one (no 35) was obtained living from the collection in the Zoological laboratory of Leyden University.

The remaining adult animals were from Messrs. SCHOLZE & PÖTZSCHKE's at Berlin.

From eggs of these latter animals larvae were grown, four of which were treated in the same way as the larvae of *Salamandra maculosa* Laur.

In some adult specimens of the animals obtained from Berlin the metamorphosis was artificially transformed by the addition of thyreoid powder to their food. This thyreoid powder was put at our disposal by N.V. Organon of Oss (Holland).

After about six weeks the gills had wholly disappeared, the gill slits closed and the tail membrane reduced. Just before the adult stage is reached a typical skinning shows itself.

Of the bigger axolotls either a segment or the heart free prepared in the pericard was fixed in alcohol of 96% or in Zenker's fixative, imbedded in paraffin or celloidin, and stained with Mallory's connective tissue staining or with haematoxylin-eosin. All this material was sectioned in transverse sections.

In table III a survey of these series is given. The celloidin series turned out very unsatisfactory as almost always gas bubbles appeared to be present in the animals during sectioning. In con-

TABLE III

Number of animal	Length of body in mm	Object	Fixative	Medium of imbedding	Staining	Thickness in micra	Part of the bloodvessel system that could be used	Stage of development at the time of killing
23	32	segment	alc. 96%	paraffin	Mallory	10	heart and arterial arches	young larvae
24	34	segment	alc. 96%	paraffin	Mallory	10	heart and arterial arches	
25	66	segment	alc. 96%	paraffin	Mallory	10	heart and arterial arches	
26	88	segment	alc. 96%	paraffin	Mallory	10&13	heart and arterial arches	
27	198	segment	alc. 96%	celloidin	haematoxylin-eosin	30	arterial arches	
28	186	segment	alc. 96%	celloidin	haematoxylin-eosin	25&30	arterial arches	neotenic animals
29	not measured	heart	alc. 96 %	paraffin	Mallory	15	heart and truncus art.	
30	not measured	heart	alc. 96%	paraffin	Mallory	15	heart and truncus art.	
31	200	segment	alc. 96%	celloidin	haematoxylin-eosin	20&30	arterial arches	swimming membrane reduced
32	190	segment	alc. 96%	celloidin	haematoxylin-eosin	30	arterial arches	tail flattened; only rest of swimming membrane during the skinning; gill slits closed
33	220	segment	alc. 96%	celloidin	haematoxylin-eosin	30	arterial arches	
34	not measured	heart	alc. 96%	paraffin	Mallory	10	heart and truncus art.	wholly transformed animals
35	232	segment	Zenker	celloidin	haematoxylin-eosin	30	heart and arterial arches	
36	138	segment	Zenker	celloidin	haematoxylin-eosin	20&25	heart and arterial arches	
37	143	segment	Zenker	celloidin	haematoxylin-eosin	25	heart and arterial arches	
38	155	heart	alc. 96%	paraffin	Mallory	15	heart and truncus art.	

sequence of this it was not in all the series possible to use the bloodvessel system wholly for our investigation.

In table III it is stated which part of the bloodvessel system of the various animals could be used for the investigation.

III. THE HEART

Shape and position of the heart

Own investigation

The parts of the heart in *Salamandra maculosa* Laur. – sinus venosus, atria, ventricle and bulbus cordis – are, already in the youngest larvae examined, situated in the same relative position as is the case with adult animals (fig. 2). In younger larvae, up to specimen no 4, these parts are situated not so compactly to each other as is the case with older larvae and adult animals.

The sinus venosus lies with its caudal part to the left, with its cranial part to the left and dorsally in respect of the ventricle. This cranial part lies also dorsally to the caudal part of the auricles. In older larval specimens (after no 5) the sinus venosus reaches a more cranial point in respect of these atria. These atria lie with their caudal part to the left, with their cranial part in front of the ventricle.

The bulbus cordis is adjacent to the right ventral wall of the atria. In older larvae this bulbus cordis has already sunk deeply into the right auricle.

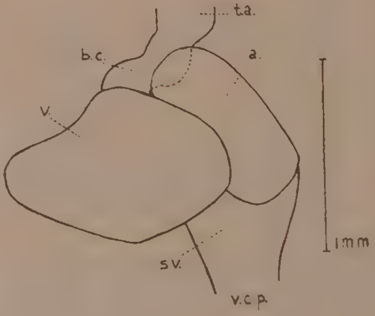

Fig. 2. Ventral view of a larval heart of *Salamandra maculosa* Laur. (no 4), graphic reconstruction. t.a., truncus arteriosus; b.c., bulbus cordis; v., ventricle; a., atria; s.v., sinus venosus; v.c.p., vena cava posterior.

The heart of the young larvae lies very much headward under the hindmost part of the skull and Atlas vertebra. In older larvae and adult animals the heart is situated more tailward under the Atlas vertebra and the second and third vertebrae, and dorsally of the coracoids. We tried to get an impression of this caudal displacement by comparing the distances of some cardiac points with respect to the backs of the occipital condyles. On the heart were taken the caudal edge of the auriculo-ventricular opening which is easily perceivable, and the apex of the ventricle. The situation of the latter point will depend on the systolic rhythm of the heart. In connection with the examination of the arterial arches–about which will be spoken later on–as one of these points the front of the bifurcation of the truncus arteriosus (bifurcation of the carotids) was chosen.

The situation of these three points with respect to the occipital condyles was determined by counting the sections of known thickness between these condyles and the observation points.

When determining the distances in micra by counting these sections a mistake may be made through the obliqueness of the series in lateral and dorso-ventral direction. The lateral obliqueness is measurable by means of the occipital condyles, so that the mistake can be partly checked. The dorso-ventral obliqueness cannot be determined for want of comparable points in dorso-ventral direction. On account of this the distances measured with respect to the occipital condyles are only approximately right.

If we want to compare these distances in different larval stages we shall also have to compare the distances between some internal points in these different stages in connection with the bodily growth. In this connection we measured in each of the animals the distance between the two planes of the lateral edges of the occipital condyles and the average distance between the backs of the foramina nervi spinalis of the second, third, fourth and fifth vertebrae.

In table IV these distances and measures are given.

From the comparison of the graphic representations of these figures as shown in fig. 3 it appears that in the youngest larvae (nos 1, 2, 3) the heart shows a growth proportional to the parts of the skeleton.

After specimen no 4 (nos 5 and 6) we find a great increase of the heart as well as of the skeleton, but the distance from the cranial point of the truncus to the occipital condyles remains the same, so that owing to growth a caudal displacement of the heart takes place.

After specimen no 6 (stage during metamorphosis) the heart is shifted in caudal direction with respect to the skeleton. This displacement does not seem dependent on the stage of the metamorphosis or the bodily growth.

TABLE IV

Number of animal	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Distance between the front of the bifurcation of the truncus arteriosus and the caudal planes of the cond. occipitales [1]	750	750	910	900	870	910	260	520	190	410	470	360	610	200	220	670	750
Distance between the caudal planes of the cond. occipitales and the caudal edge of the auriculo-ventricular opening	40	210	270	20	690	830	1490	1320	1480	1630	990	1490	970	1360	1250	350	180
Distance between the caudal planes of the cond. occipitales and the apex of the ventricle	300	780	830	560	1710	1930	2130	2170	2300	2290	1770	2260	1560	1880	2250	1210	990
Average distance between the backs of the foramina nervi spinalis of vertebrae II, III, IV and V	380	430	460	590	640	700	690	690	760	660	690	790	710	610	620	600	570
Distance between the two planes of the lateral edges of the cond. occipitales	780	870	930	1120	1240	1440	1290	1360	1390	1230	1200	1450	1440	1290	1290	1240	1130

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[1]) all distances in micra

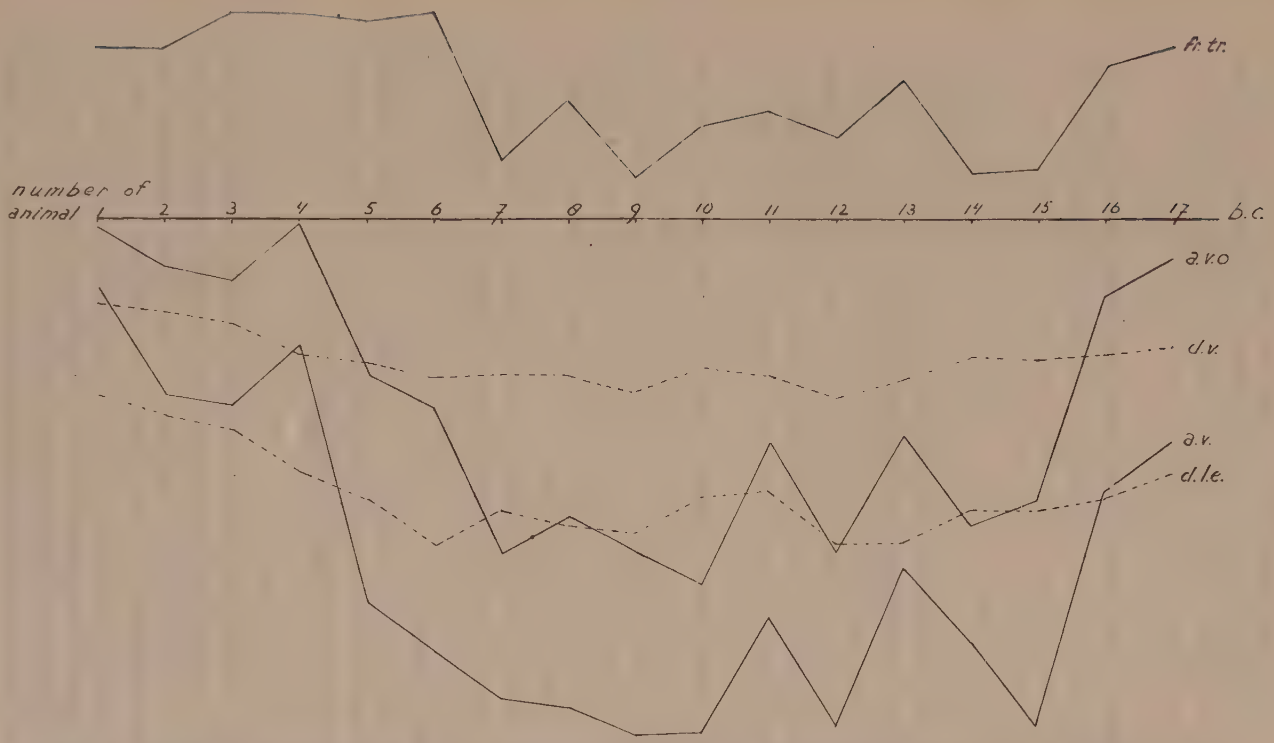

Fig. 3. Graphical representation of the position of the heart of *Salamandra maculosa* Laur. in relation to the occipital condyles.

b.c., backs of the occipital condyles; fr.tr., position of the front of the bifurcation of the truncus arteriosus; a.v.o., position of the caudal edge of the auriculo-ventricular opening; a.v., position of the apex of the ventricle. Distances between d.v. and b.c. showing the average distances between the backs of the foramina nervi spinalis of vertebrae II, III, IV and V. Distances between d.l.e. and b.c. showing the distances between the two planes of the lateral edges of the occipital condyles.

This caudal movement of the heart also continues after metamorphosis, so that in the adult animals the bifurcation of the front of the truncus arteriosus lies more caudally in respect to the occipital condyles (fig. 24).

The shape of the heart in *Ambystoma mexicanum* Shaw generally corresponds with the situation in *Salamandra maculosa* Laur.

In the youngest larvae the parts of the heart do not yet lie compactly in respect to each other; however, in the neotenic animals already the parts of the heart are situated much more closely to each other, so that here the shape of the heart is the same as in the transformed specimens.

In connection with the fact that the complete heart could not always be used (and thus neither the caudal edge of the auriculo-ventricular opening nor the apex of the ventricle), the bifurcation of the truncus arteriosus was invariably chosen as point of comparison for the determination of the position of the heart to the occipital condyles.

In very young larvae (nos 23, 24, 25 and 26) the heart also here undergoes an increase in comparison with the skeleton, so that only a seeming caudal movement takes place in these young larvae.

Contrary to this the heart has also absolutely moved caudally in older larvae (nos 27 and 28).

In the stages during metamorphosis this is still more intensively perceivable, while also here in the adult transformed animals the truncus arteriosus is situated caudally in respect to the occipital condyles (fig. 26).

So contrary to the situation in *Salamandra maculosa* Laur. the absolute caudal movement begins here far before the appearance of the first phenomena of metamorphosis.

Discussion

Hochstetter (1906) gives remarks about the changes in the position of the parts of the heart to each other in young larvae of *Salamandra atra* from 5.5–13 mm. In the older larvae of the specimens examined by us the changes as described by him continue to some extent.

Greil (1903 A) supposes a caudal movement of the heart in larvae of *Salamandra atra* from 6 to 10 mm.

We found it in much bigger larvae of *Salamandra maculosa* Laur.

and *Ambystoma mexicanum* Shaw. However, it is not impossible that the caudal movement of the heart as described by us was preceded by a previous one.

Körner (1938) describes the heart of the only transformed axolotl examined by him as being smaller than the one of the two neotenic specimens. This statement we could not confirm, as this difference is hardly demonstrable.

Sinus venosus

Own investigation

Already with the youngest of the larvae of *Salamandra maculosa* Laur. examined the sinus venosus has the typical shape which we also find in the adult animals. It consists of a conical bag, the caudal apex of which changes confluently into the vena cava posterior. With a very wide ostium the sinus venosus opens into the right atrium. The sinus is, especially in the younger specimens, triangular in the transverse section, so that one of the sides is dorsal. In older specimens this transverse section is oval, with its long axis horizontal. The caudal part of the sinus is always situated to the left, the cranial part to the left and dorsally in respect to the ventricle. The most cranial part is lying dorsally in respect to the caudal part of the auricles. With older animals the sinus is lying more cranially compared with the atria than in younger larvae. Into this anterior part enter the two ducts of Cuvier. In the youngest larvae the left duct of Cuvier is lying much more caudally than the right one; in older specimens the situation is reversed. Especially in the older specimens and in the adult animals this right duct of Cuvier is lying in about the same transverse plane as the ostium sinus venosi. Valves are not found in the openings of the ducts of Cuvier into the sinus venosus.

The wall of the sinus is smooth in the younger larval specimens and contains an endothelium. On the inner wall of the sinus venosus of older larvae and adult animals no continual layer of endocardium was perceivable – contrary to the inner walls of the ventricle and bulbus cordis. The observation is very difficult owing to the sinus venosus being filled with bloodcorpuscles. The inner wall does, however, contain endocardium layers locally, about which we shall speak later on. In older larvae the wall contains a thin stratum of muscular elements arranged in transverse direction. Trabeculae on this inner wall are not found in the

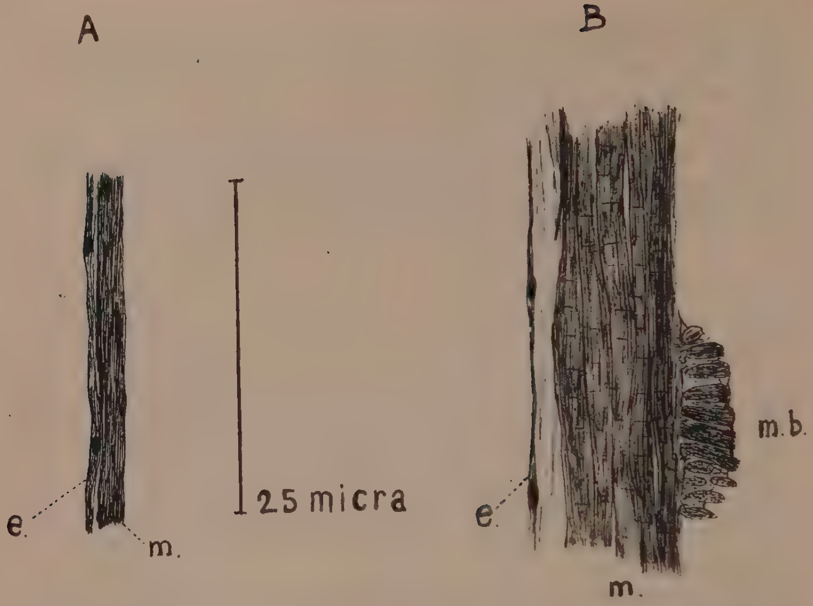

Fig. 4. Transverse sections through the wall of the sinus of *Salamandra maculosa* Laur.

A. Specimen no 7 (during metamorphosis).
B. Adult animal.

e., epicardium; m., myocardium; m.b., longitudinal muscular band.

larvae. In the adult animals this stratum is thicker and consists of striped fibres, arranged transversely. On the inside of the stratum are found very few muscular bands, arranged longitudinally (fig. 4). The muscular elements on the sinus wall decrease in number in caudal direction.

In the direct neighbourhood of the ostium sinus venosi in older larvae and adult animals the muscular stratum (myocardium) is thicker than in the rest of the sinus venosus and forms a few muscular trabeculae, situated on the inner wall of the sinus venosus. This ostium is, in all animals examined, surrounded by an annular ridge on the internal wall of the heart, in which, especially in the caudal part, many muscular elements are lying. In respect to the two atria this opening lies in the caudal base – wholly to the left in the right atrium – directly beside the attachment of the septum atriorum in the atrium wall.

On the dorsal wall of the sinus venosus is lying the vena pulmonalis. This vena pulmonalis is in older larvae much wider

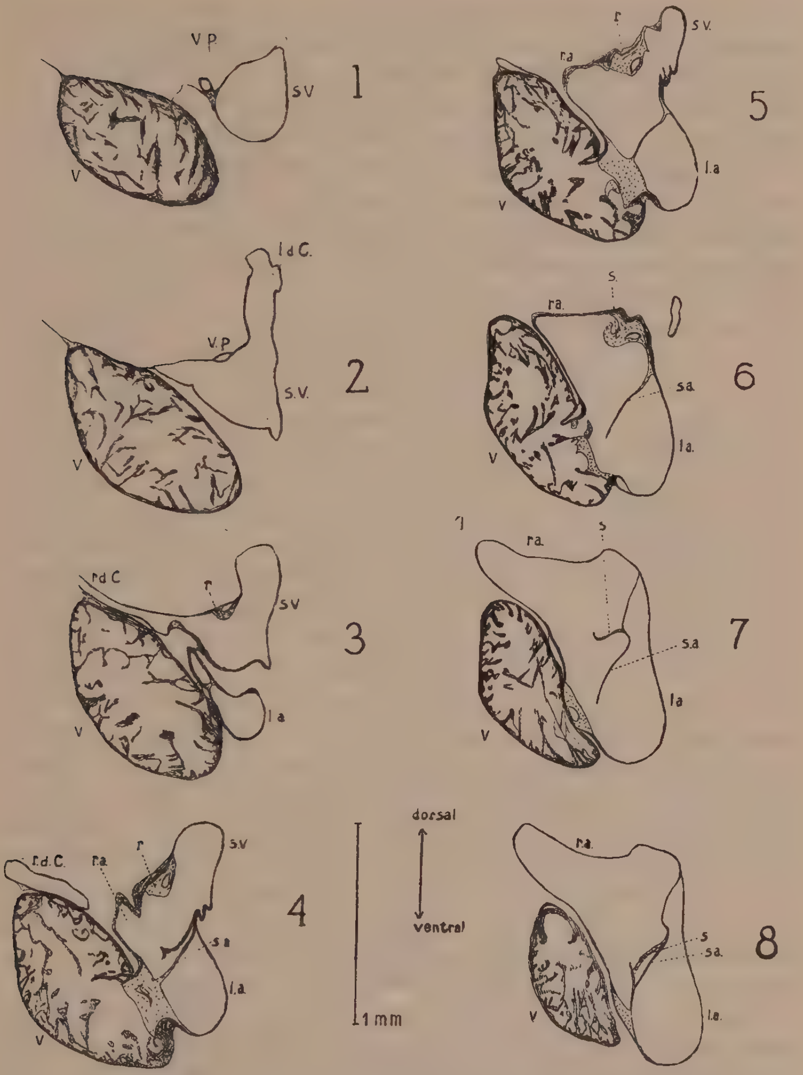

Fig. 5. Transverse sections through a larval heart of *Salamandra maculosa* Laur. (no 2).
1 to 8 = caudal to cranial.
v., ventricle; s.v., sinus venosus; v.p., pulmonary vein; l.d.C., left duct of Cuvier; r.d.C., right duct of Cuvier; r., ridge of the pulmonary vein; r.a., right atrium; l.a., left atrium; s., sinus flap; s.a., septum atriorum.

(fig. 5, 6, 7, 8) than in younger specimens. As regards its situation this vena pulmonalis runs, in all specimens, over the dorsal wall of the sinus from the right caudally to the left cranially and in the cranial part it has even sunk into this wall, and is lying in the inner layer of this dorsal sinus wall protruding into the cavity.

The vena pulmonalis crosses along the inside of the dorsal wall of the ostium sinus venosi – in a few specimens over a short part of the dorsal wall of the right atrium – to touch the septum atriorum and to enter into the atrium sinistrum immediately to the left of the septum.

The relation between this vena pulmonalis, the ostium sinus venosi and the septum atriorum is, in our opinion, very important from a comparative anatomical point of view.

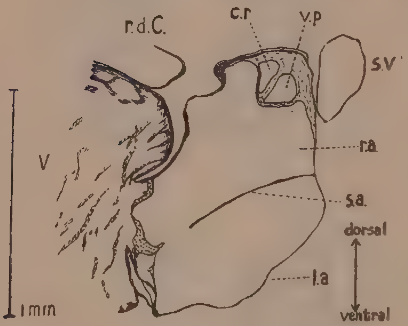

Fig. 6. Transverse section through a larval heart of *Salamandra maculosa* Laur. (no 5).
v., ventricle; s.v., sinus venosus; r.a., right auricle; l.a., left auricle; s.a., septum atriorum; v.p., pulmonary vein; c.r., cavity of the ridge; r.d.C., right duct of Cuvier.

In the younger specimens (nos 1 and 2) the vena pulmonalis does not touch the outside of the caudal part of the sinus. In a transverse plane with the opening of the left duct of Cuvier the vena pulmonalis sinks into the wall of the sinus, and lies in the cranial part over a short length in a ridge, bordered by connective tissue (endocardium), on the inner wall of the sinus venosus. In the youngest larva this border is only very thin. This border of connective tissue lies for the greater part to the right of the vena pulmonalis. Following up the border from caudally to cranially, we find in the cranial sections a cavity to the right of the vena pulmonalis. In a transverse plane with the ostium sinus venosi the right wall of this cavity gets detached from the wall of the sinus, so that a flap of the connective tissue border round the vena pulmonalis protrudes in the ostium. Where the vena pulmonalis touches the septum atriorum this protruding flap is attached to the septum atriorum. Cranially the free end of this flap is for a short distance connected with the septum atriorum (fig. 5, no 8).

In specimens which are slightly older (nos 3, 4, 5) the sinus venosus is lying more cranially as compared with the atria. The right part of the endocardium ridge of the vena pulmonalis is already in its caudal part hollow (fig. 6), and changes cranially into a short flap which extends farther into the heart cavity than in the younger specimens. Its caudal margin is for a greater distance attached to the septum atriorum.

In one of these specimens this attaching-part of the sinus flap stretches to the free margin of the septum atriorum. This free end is connected with the ventral auriculo-ventricular valve. This same relation was also found in some older larvae.

These older larval specimens are difficult to arrange in a definite order from the point of view of the development of the peculiarities described above. In these older larval specimens the sinus venosus extends more cranially with respect to the atria. The opening of the right duct of Cuvier lies in about the same transverse plane as the ostium sinus venosi. These openings of the ducts of Cuvier are in these larvae lying completely in the

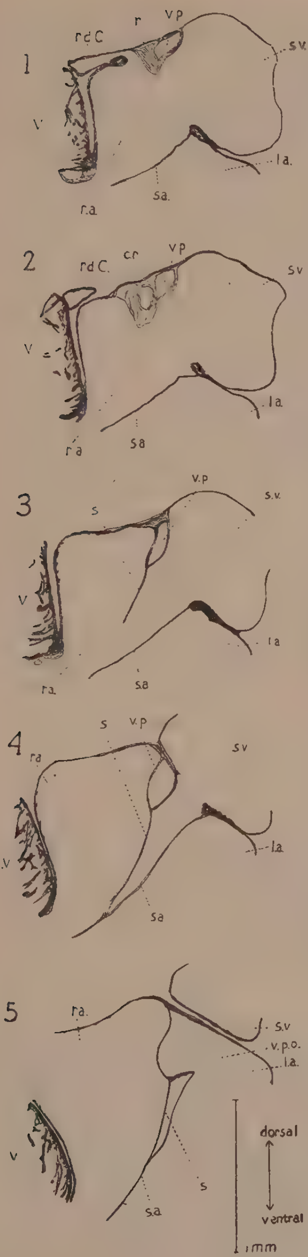

Fig. 7. Transverse sections through a larval heart of *Salamandra maculosa* Laur. (no 8). 1 to 5 = caudal to cranial.

v., ventricle; s.v., sinus venosus; v.p., pulmonary vein; r., ridge of pulmonary vein; c.r., cavity of the ridge; r.d.C., right duct of Cuvier; r.a., right auricle; l.a., left auricle; s., sinus flap; s.a., septum atriorum; v.p.o., opening of the pulmonary vein into the left auricle.

cranial angles of the sinus venosus. In some of these larvae the border of connective tissue to the right of the vena pulmonalis has totally disappeared, so that the connection of the vena pulmonalis with the dorsal sinus wall seems smaller. Of course, in these specimens we find the cavity of this ridge left. The walls of the cavity contain fibres. In relatively more caudal sections than in younger larvae the right wall of the cavity gets detached from the sinus wall. The resulting flap extends farther into the heart cavity and is lying even partly in front of the ostium sinus venosi (fig. 7, no 3). In one of the larvae (no 13) it lies even wholly in front of it. Whereas the connection of the flap with the vena pulmonalis has decreased, the ventral attaching-part of the sinus flap with the septum atriorum has grown much longer.

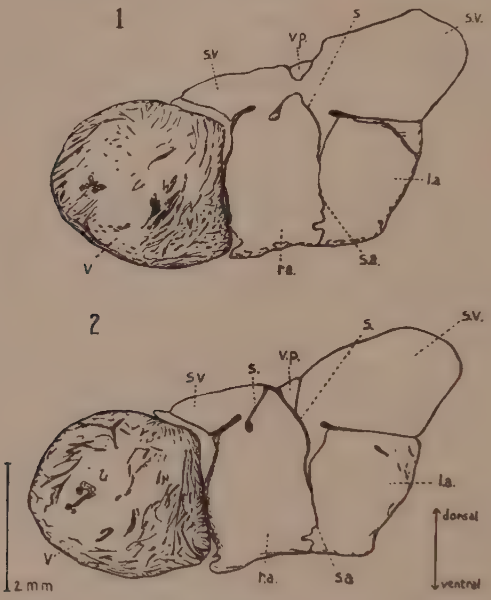

Fig. 8. Transverse sections through the heart of an adult *Salamandra maculosa* Laur. (no 18).
1 = caudal; 2 = cranial.
v., ventricle; s.v., sinus venosus; r.a. right auricle; l.a., left auricle; s.a., septum atriorum; s., sinus flap; v.p., pulmonary vein.

In the adult animals we find the vena pulmonalis only in its most cranial part situated in the wall of the sinus venosus. The connective tissue border is no longer present. The aperture of the right duct of Cuvier lies in the same place as described in the older larvae. The ostium sinus venosi is caudally covered by a flap which is over a great length connected with the septum atriorum. At its free margin this flap is thickened by connective tissue and muscle fibres (fig. 8).

The cranial part of the flap attaches itself with its middle part to the wall of the vena pulmonalis, so that this cranial part in transverse section is separated into a left part and a right one (fig. 8, no 2).

The smaller right part closes the right half of the ostium sinus venosi and alters cranially into the atrium wall. The greater left part lies in front of the left half of the ostium sinus venosi and is attached between the vena pulmonalis wall and the septum atriorum (fig. 8, no 2).

This vena pulmonalis crosses the cranial wall of the ostium sinus venosi and enters into the left atrium beside the attaching point of the septum.

From the relation described we may conclude that the sinus flap arises from the connective tissue ridge beside the vena pulmonalis as found in the larvae.

The position of the sinus venosus in *Ambystoma mexicanum* Shaw corresponds with that of *Salamandra maculosa* Laur.

In the young larvae the vena pulmonalis lies already in the most caudal part of the sinus venosus on the outer wall of the sinus venosus. Only in the cranial part of the sinus venosus the pulmonary vein lies on the inner wall of the sinus venosus. The vena pulmonalis is very narrow. Only in its most cranial part it has a slight connective tissue border. After specimen no 25 we find in the larval specimens and in the transformed animals a slightly developed short sinus flap on the septum atriorum. Compared to *Salamandra maculosa* Laur. this flap is much shorter. This flap can be wholly absent in adult specimens of *Ambystoma mexicanum* Shaw (nos 36 and 38).

As regards the structure of the sinus venosus the neotenic animals correspond with the transformed ones.

The vena pulmonalis has become much wider in older animals, and is situated more caudally on the inner wall of the sinus venosus.

The longitudinal muscular bands on the inner wall of the sinus venosus seem to us to be present to a less extent than in *Salamandra maculosa* Laur.

Discussion

Data about the structure of the wall of the sinus venosus in *Salamandra maculosa* Laur. we find in BRUNER (1900) and FRANCIS (1934). BRUNER (1900) finds that the sinus venosus is provided with muscular walls. FRANCIS (1934) finds no striped muscle fibres in the sinus wall. In contrast with this we found that in the older larval specimens muscle fibres on the thin wall are present. In the adult forms these fibres are present to a greater extent and besides striped. It is even possible to find a slight structure of trabeculae by the presence of longitudinal muscular bands.

The course of the vena pulmonalis from caudally right to cranially left, but also the tense contact of the cranial part in the wall of the sinus venosus we already find in BRUNER (1900), ZÜLLICH (1930), FRANCIS (1934) and KÖRNER (1938).

Whereas RÖSE (1890) describes the same relations in *Sieboldia maxima* (*Cryptobranchus japonicus*) and *Siredon pisciformis* (larva) he states for Salamandridae – of which he only examined one specimen of *Triton cristatus* and one larva of *Salamandra maculata* – that the vena pulmonalis has not grown together with the wall of the sinus venosus but runs freely across it.

HOCHSTETTER (1906) describes the development of the heart of embryos of *Salamandra atra* from 5.5 mm onwards. In accordance with FEDEROW (1910) he finds in very young urodelan embryos the vena pulmonalis entering the sinus venosus. Both of them point out the concurrence in the course and the ending of the vena pulmonalis of urodelan embryos and the similar relations as described by RÖSE (1890) and BOAS (1880) for Dipnoi.

None of these authors gives a description of the border of connective tissue, found by us in young larvae, round – but especially to the right of – the proximal part of the vena pulmonalis.

FEDEROW (1910, p. 557) examining the development of the lung vein of young embryos of *Rana temporaria* (4 mm–11.7 mm) and of *Triton taeniatus* (8.7 mm–14.6 mm), speaks of "eine Proliferation des Endothels" in the dorsal wall of the sinus venosus. The relation of the vena pulmonalis he describes as follows:

"Ferner sieht man im Centrum der Proliferation die Vene in Form einer kleinen hohlen Ausstülpung der endothelialen Sinuswand".

Possibly this endocardium ridge may also be compared with the structure as described by Röse (1890) and Boas (1880 and 1883) in the heart of Dipnoi in connection with the initial stage of the septum atriorum. This same thought is in our opinion also present in Benninghoff's (1933, p. 489 and 490) description of the origin of the septum atriorum in Urodela: "Die ersten Stufen dieses Septums traten uns bei den Dipnoern (*Ceratodus* und *Protopterus*) entgegen, sie bestanden aus dem dorsalen Endokardwulst des Ohrkanals und der sogenannten Pulmonalfalte, die die Pulmonalismündung rechts begrenzt und mit dem Endokardwulst verwachsen war. Diese Pulmonalfalte ist eine kurze trennende Wand zwischen Sinus- und Pulmonalismündung, sie kann als eine Gefässporn aufgefasst werden, der durch die Verwachsung mit dem dorsalen Endokardwulst fixiert wird und den Wulst weiter ergänzt."

From our description it appears that there is a strong relation between this ridge and the sinus flap, so that in our opinion this flap arises from scooping out and caudal lengthening of this ridge. Also in adult animals this valve is found attached to the vena pulmonalis wall so that it is cranially divided into a larger left part and a smaller right one, which parts are caudally connected with each other, so that one flap appears in front of the ostium sinus venosi.

Röse (1890), in the forms examined by him – among which one larval *Siredon pisciformis* and one larva of *Salamandra maculata* – describes two valves, of which the left valve is slightly larger than the right one. In the adult animals of *Salamandra maculosa* the ostium sinus venosi should, according to Bruner (1900), be closed by two valves, one of these valves being rudimentary or completely absent, the other reaching as a membrane up to the auriculo-ventricular opening. Züllich (1930) and Francis (1934) describe the closing of the sinus by means of a side-flap of the septum atriorum. From their description it does not appear, however, that they have made microscopic investigations of the closing of the sinus.

Körner (1938) microscopically examined the hearts of two specimens of *Salamandra maculosa* and three specimens of *Ambystoma mexicanum.* He finds, together with all the Urodela he examined, – except the lungless salamanders and *Proteus* – this sinus closed by a large side-flap attached to the septum atriorum. For *Ambystoma mexicanum* KÖRNER finds in one neotenic axolotl one very small sinus valve, in another a larger valve.

In connection with our investigation it is of the greatest importance that BRUNER (1900) and KÖRNER (1938) always find this sinus flap also attached to the vena pulmonalis wall. This relation KÖRNER (1938, p. 150) describes as follows: "Die Vena pulmonalis tritt von kaudal und dorsal an den Sinus venosus heran, verläuft in der unteren und dorsalen Wand des Sinus aufwärts, und zieht schräg nach rechts kranial durch die Sinusöffnung zum linken Vorhof, indem sie die am dorsalen und dorsalen unteren Umfange der Sinusöffnung angeheftete Basis der Sinusklappe als Brücke benutzt."

In the literature we find only very vague references to the origin of the closing of the sinus in Urodela. HOCHSTETTER (1906) only remarks that the development of the sinus valves of salamanders happens in the same way as in Selachii, where between the sinus wall and the atrium folds are formed that are the origin of the sinus valves. BENNINGHOFF (1933) says that in young larvae there are endocardium cushions on these folds. KÖRNER (1938) finds in a *Pleurodeles waltlii* of 8 mm (just after metamorphosis) a sinus valve lying only as a very short flap on the right side of the septum atriorum.

A relation between this flap and the vena pulmonalis of this animal is, however, not described by KÖRNER in details.

Atria

Own investigation

The atria in *Salamandra maculosa* Laur. are situated with their caudal parts to the left, with their middle parts to the left and dorsally, with their cranial parts a little to the right and cranially as regards the ventricle. The cranial apex of the atria is found in the youngest specimens near the alteration of the bulbus cordis into the truncus arteriosus. In older larvae and adult animals this apex extends a little more cranially than the point of transition described above.

The shape of the atria is strongly dependent on their being filled with blood or not. Thus the ventral right wall of the right atrium is in empty hearts pressed inwards by the bulbus cordis.

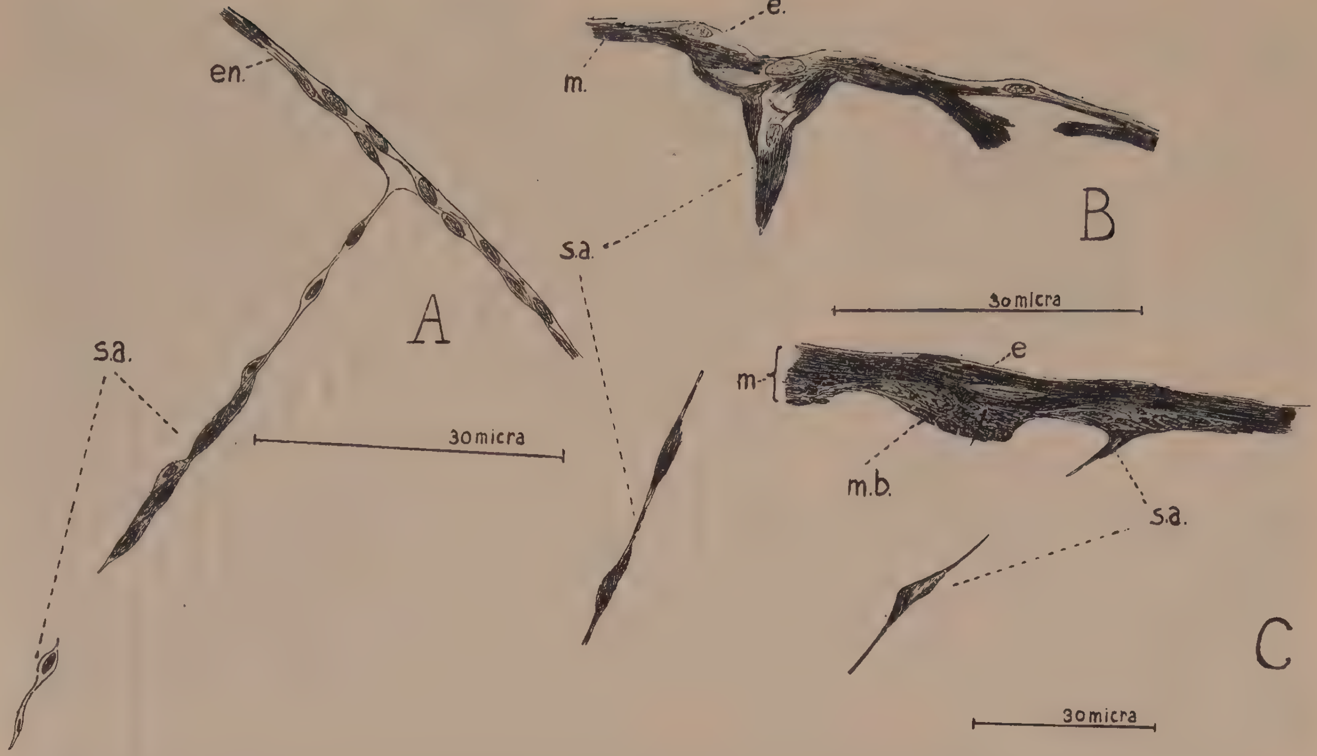

Fig. 9. Transverse sections through the wall of the auricles and the septum atriorum of *Salamandra maculosa* Laur. A. Before metamorphosis (no 1). B. During metamorphosis (no 6). C. Adult animal. en., endothelium; e., epicardium; m., myocardium; m.b., longitudinal muscular band; s.a., septum atriorum.

In filled hearts, also with adult animals, this inward curving is only slightly noticeable. Both atria are funnel-shaped in the direction of the auriculo-ventricular opening. This auriculo-ventricular opening lies with respect to the longitudinal axis of the body slanting from right to left and also from cranially ventral to caudally dorsal.

The atria are divided by the septum atriorum into a large right and a much smaller left atrium. This septum atriorum is in all series examined bulging into the left atrium. Its free margin is in an arched way stretched out across the auriculo-ventricular opening. The dorsal and ventral edges are attached to the dorsal and ventral auriculo-ventricular valves. In the caudal part of the right atrium beside the septum atriorum lies the ostium sinus venosi. Slightly more cranially lies the opening of the vena pulmonalis into the left atrium. Valves are not found in this latter opening.

The walls of the atria are showing hardly any differentiation in our youngest specimens (nos 1–5). This wall possesses in the caudal part of the atria muscular fibres lying circularly around the auriculo-ventricular opening. In the rest of the atrium wall very few muscular fibres are differentiated in transverse direction (fig. 9, A). Only in the cranial part we find, besides non-differentiated cells, a few muscular bands protruding into the cavity of the atria. In older larvae (fig. 9, B) a transversal interior layer of muscular fibres has arisen, on which trabeculae appear – especially in the cranial part – in the dorsal and right walls of the atrium. These trabeculae project already far into the atrium lumen and form a network on the atrium wall. As the larvae are growing older there appear on the caudal part, too, trabeculae on the inner wall of the atrium, which are on the whole arranged longitudinally. Only in the adult animals (fig. 9, C) we find these longitudinal bands on the left ventral wall of the atrium. In the direct neighbourhood of the auriculo-ventricular opening these bands are bent with the muscular ring of the auriculo-ventricular opening (Annulus atrioventricularis, Benninghoff, 1922). In agreement with the observations on the wall of the sinus venosus, on the inner walls of the atria also no continual layer of endocardium was perceivable.

The septum atriorum is attached to the dorsal left and ventral right atrium walls. In the specimens before metamorphosis (nos 1–5) the caudal part of the ventral septum attachment to the atrium wall is provided with an endocard thickening, which disappears cranially and changes caudally gradually into the ventral auriculo-ventricular valve (fig. 5). In older larval specimens only a rest of this ventral endocard thickening is found. The dorsal attachment of the septum atriorum, too, is connected with the dorsal auriculo-ventricular valve. Endocard thickenings are not present at the caudal part of this dorsal septum attachment. This caudal part of the attachment of the septum atriorum to the dorsal left atrium wall extends along the left edge of the ostium sinus venosi (fig. 5 and 7).

In our specimen no 1, cranially in respect to this ostium, we find the left part of the endocard ridge of the vena pulmonalis, which is very broad here, connected with the septum atriorum (fig. 10, A). The right part of the ridge bears the initial stage of the sinus valve. The left part of the endocard border enters cranially into relation with the septum atriorum. Following up this endocard thickening there appears cranially a cavity directed towards the left atrium. Into this cavity the vena pulmonalis

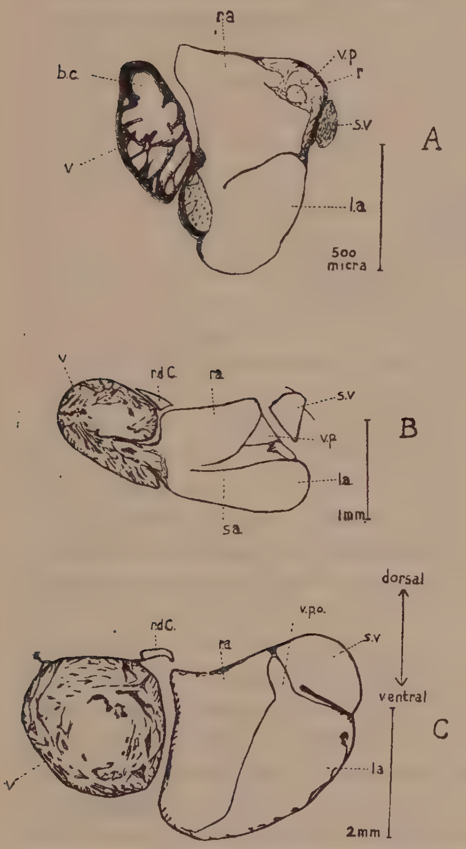

Fig. 10. Transverse sections through the the hearts of *Salamandra maculosa* Laur.
A. Stage before metamorphosis (no 1).
B. Stage during metamorphosis (no 7).
C. Adult animal.
v., ventricle; l.a., left atrium; r.a., right atrium; s.a., septum atriorum; r.d.C., right duct of Cuvier; v.p., pulmonary vein; r., ridge of the pulmonary vein; v.p.o., opening of the pulmonary vein into the left atrium; s.v., sinus venosus; b.c., bulbus cordis.

enters. The wall of the lung vein then changes gradually into the septum atriorum. In this specimen the septum atriorum is for a long distance cranially, in respect to the opening of the vena pulmonalis, attached to the atrium wall by an endocard thickening.

In somewhat older specimens (nos 2–5) we find the same relation of the peculiarities as described above. The hollowing out of the endocard thickening, caudally in respect to the vena pulmonalis opening, increases and the septum atriorum is cranially, in respect to the vena pulmonalis, not connected by an endocard attachment.

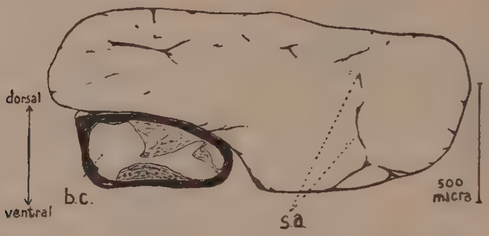

Fig. 11. Transverse section through the cranial part of the auricles. *Salamandra maculosa* Laur. (no 10).
b.c., bulbus cordis; s.a., septum atriorum.

In specimens older than no 5 the endocard thickening, connected with the vena pulmonalis and the septum atriorum, has all but disappeared (fig. 10, B). Cranially in respect to the ostium sinus venosi, we find in adult animals the septum atriorum bending funnel-shaped to the opening of the vena pulmonalis (fig. 10, C). From this description it is evident that the funnel-shaped narrowing of the left atrium to the vena pulmonalis opening arises from the disappearance of the endocard masses as found in younger larval specimens (before metamorphosis) caudally in respect to the vena pulmonalis opening.

The structure of the septum atriorum undergoes some remarkable changes. This septum consists in the youngest specimen (no 1) in a layer of one or two cells' thickness. In the cranial part there are some muscular fibres. In this specimen openings in this septum are only present in an extremely small number (this specimen no 1 containing but three openings), lying especially in the cranial part. It is remarkable that these openings are situated in the direct neighbourhood of the sparsely developed muscular fibres (fig. 9, A).

In somewhat older specimens (nos 2–5) we find some more muscular fibres, especially in the cranial part of the septum, and here, too, we see only very few openings (fig. 9, B). In specimens older than no 5 the septum atriorum has the structure of that of the adult animals (fig. 9, C). It possesses a network of muscular bundles, most strongly in the cranial part. Between the small mazes a thin layer remains left. Especially in this cranial part we clearly find openings in the septum atriorum. These openings are, it is true, not numerous, but very clear and have different diameters. The placing of the openings is not the same in different specimens. Especially in the most cranial part of the septum the openings are very wide. Here the septum gradually changes into the musculature of the cranial atrium wall (fig. 11). As appears also from this description we can, when studying the septum atriorum in successive stages, hardly get away from the impression that there is a relation between the muscularisation and the perforation of the septum atriorum.

In *Ambystoma mexicanum* Shaw, too, we find already in young larvae (nos 25 and 26) openings in a small number present in the septum atriorum. These openings are situated especially in the cranial part of the septum atriorum, in which also muscular elements are noticeable.

In the neotenic and transformed animals the openings are present in a greater number, although in our opinion less than is the case in adult *Salamandra maculosa* Laur.

The atria in neotenic animals correspond with the atria of the transformed animals in structure.

In many specimens the septum atriorum is bent in front of the opening of the sinus venosus into the right atrium.

Discussion

The arrangement of the muscular bands on the inner wall of the atria of *Salamandra maculosa* Laur. as described by us, we also find for the same species in Körner (1938). Körner, too, did not draw an endocardium layer on the inside of the atrium wall. Contrary to Francis (1934) we are of the opinion that no bulges (recesses) appear on the walls of the atria in contracted condition.

According to the investigation of HOCHSTETTER (1906) and BENNINGHOFF (1922), also stated by GRAHAM KERR (1919) the atrial septum arises as a ridge of endocardium which projects into the lumen from the cranial wall. The concave free edge of this grows towards the auriculo-ventricular opening, while its ventral base of attachment becomes continuous with the ventral auriculo-ventricular cushion, and its dorsal base of attachment becomes continuous with the dorsal auriculo-ventricular cushion. BENNINGHOFF (1933, p. 490) says of this septum atrium: "Ontogenetisch entsteht das Septum als Endokardsichel, die ihre Fusspunkte in dem ventralen und dorsalen Endokardkissen hat und so entlang dem Dach des Vorhofs eine Verbindung zwischen den beiden Kissen herstellt. Diese Verbindung konnte entstehen, nachdem der besagte Gefässporn ein Stück weit die Brücke geschlagen hatte." [1])

As appears from our description of *Salamandra maculosa* Laur. the vena pulmonalis ridge is connected with the septum atriorum and in older specimens the wall of the vena pulmonalis is partly concerned in the shaping of the septum atriorum. As has already been stated in the description of the sinus venosus, the sinus valve arises from the right part of the connective tissue ridge, while the left part leads to the shaping of the vena pulmonalis funnel. How far, however, this vena pulmonalis ridge forms a bridge at the shaping of the septum atriorum, as BENNINGHOFF writes, does not appear from literature, nor is it determinable from our specimens examined.

According to HOCHSTETTER (1906) and FEDEROW (1910) the lung vein in very young larvae enters into the sinus venosus. This opening shifts cranially. FEDEROW (1910) found in larvae of *Triton taeniatus* this opening in the left auricle – while also the edge of the developing septum atriorum has then reached this opening. In consequence of FEDEROW's investigation KÖRNER (1938), too, surmises that the vena pulmonalis should be determinative for the origin of the caudal part of the septum atriorum; so that, when the lung vein is lacking, as is the case in lungless salamanders, this caudal part does not come to any development.

According to KÖRNER, then, the cranial part of the septum atriorum should be supplemented by the sinus valve. From our investigation, however, it appears that this very sinus valve arises from the border of the vena pulmonalis, and that therefore this valve could probably not come to any development if in larval specimens the border of the vena pulmonalis should be lacking (which may be the case in larvae of lungless salamanders, although this has not yet been examined).

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[1]) See quotation from BENNINGHOFF mentioned in the "Discussion" dealing with the sinus venosus.

In connection with this great doubt may arise whether KÖRNER's statement about the structure of the septum atriorum in lungless salamanders is correct.

The structure, especially the perforation of the septum atriorum, in adult Urodela, is very much disputed in literature. As to *Salamandra maculosa* LANGERHANS (1873), BOAS (1883), BRUNER (1900), NOBLE (1925) and KÖRNER (1938) describe the septum as being more or less perforated with openings of various diameters. SABATIER (1873), ZÜLLICH (1930), and FRANCIS (1934) did not find any opening in this septum atriorum. In our opinion only microscopic observations of transverse sections can be conclusive for a decisive determination. In all the older animals examined of *Salamandra maculosa* Laur. openings of the same nature were clearly perceivable.

BOAS (1883) found small openings sparsely present in the septum atriorum of *Siredon*. KÖRNER (1938), too, found openings in the septum atriorum of neotenic *Ambystoma mexicanum*. In the same way we find openings in the septum atriorum of *Ambystoma mexicanum* Shaw, however, to a less extent than in *Salamandra maculosa* Laur.

HOCHSTETTER (1906) did not find any openings in the larval specimens of *Salamandra atra* which he examined, so that in literature it is always supposed that they arise secondarily. This opinion we can fully confirm. NOBLE (1925) found the septum atriorum complete, without openings, in larvae of *Amblystoma paroticum* and *Dicamptodon ensatus* Eschscholtz, but also (1925, p. 393) in the "recently metamorphosed *Amblystoma tigrinum*". In the larval specimens of *Salamandra maculosa* Laur. and *Ambystoma mexicanum* Shaw as examined by us the perforation appears already before and during metamorphosis. In our opinion there is a direct relation between the muscularisation and the perforation of the septum atriorum. This opinion seems to be confirmed by NOBLE (1925), who in *Rhyacotriton olympicus* Gaige also found that the septum atriorum was greatly fenestrated, while also in these animals muscular bundles on the septum atriorum, as seen in lunged salamanders, were proportionally larger, just as he found openings in the septum atriorum of *Ambystoma tigrinum* Green shortly after metamorphosis when the muscular fibres appear to group into bundles.

Ventriculus

Own investigation

Externally in a ventral view the ventricle has a conical shape, the top of which is situated caudally and slightly to the right of the median line. The cranial and left base of the ventricle is ovally-shaped and is lying in the animal slanting from right cranially to left caudally, but also slightly from cranial dorsally to caudal ventrally. In the ventral part of this base is lying the ostium atrio-ventriculare. This ostium is overarched by the edges of the ventricle, so that the atrium seems to have sunk into the ventricle. On the borderline of the atrium and ventricle a deep

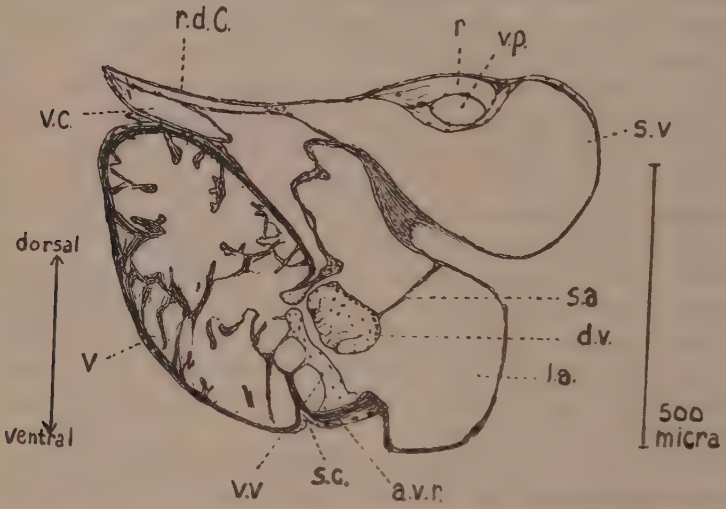

Fig. 12. Transverse section through a larval heart of *Salamandra maculosa* Laur. (no 1).
v., ventricle; s.c., sulcus coronarius; a.v.r., auriculo-ventricular ring; d.v., dorsal valve; v.v., ventral valve; l.a., left atrium; s.a. septum atriorum; s.v., sinus venosus; v.p., pulmonary vein; r., ridge of the pulmonary vein; r.d.C., right duct of Cuvier; v.c., vena cordis.

furrow is formed, called the sulcus coronarius (sulcus atrioventricularis). In the right part of the ventricle, cranially to the ostium atrio-ventriculare the bulbus cordis arises.

This external shape undergoes few changes during the development. The apex is in the youngest specimen examined still very blunt and becomes sharper with the growing older of the animals. The cranial ostium ventriculare bulbi (ostium arteriosum) lies in the youngest larvae dorsally and to the right of the ostium atrio-ventriculare.

In older larvae than specimen no 5 this latter ostium lies more cranially but at the same time much less dorsally from the ostium atrio-ventriculare.

So we see that in general the increase of the ventricle as compared with the other parts of the heart takes place by an increase of its longitudinal axis, while this axis, which in young specimens is slanting from cranial dorsally to caudal ventrally, obtains a smaller slope.

The change of the atrium wall into that of the ventricle has already been partly described with the atria. The muscular bundles of the atrium wall are arranged in a circular way around the ostium atrio-ventriculare. In the direction of the ventricle this wall grows thinner and round the ostium it forms a fold, the caudal wall of which changes into the wall of the ventricle (fig. 12 and 13). The furrow of the sulcus coronarius is deep and filled with epicardial connective tissue.

In the auriculo-ventricular opening three valves are generally present, arranged with their bases of attachment against the atrioventricular ring. In the youngest specimen already we find one large dorsal valve, one great ventral valve and a much smaller right lateral valve (fig. 12). In the youngest larvae the dorsal and right lateral valves posses a very thick endocardial attachment, so that their hollowness is only very slightly developed. The endocardial attachment edges of the valves are connected with each other by a very thin endocard layer. The valves have an arching surface directed to the atria and are scooped out on the underside directed to the ventricle, especially in the older animals.

By thin endocardial fibres, the chordae tendineae, this inside directed to the ventricle is connected with the fold of the atrium wall and the longitudinal ventricle trabeculae. The structure of the valves and of the chordae tendineae, which in the young specimens consists in a homogeneous connective tissue, becomes fibrous in the older animals. We cannot discover any muscular elements in this structure. The dorsal and ventral valves are in a few larvae connected by a small endocard ridge at the left lateral ostium edge. In the adult animals this ridge is more strongly developed and can, by containing a small hollowness even take the structure of a left lateral valve. The cavity of the ventricle is, from the ostium atrio-ventriculare to the entrance of the bulbus cordis, more or less L-shaped. This space is surrounded by a spongy musculature, consisting of septa arranged chaotically and enclosing larger or smaller chambers (fig. 13). This spongy structure is developed most strongly in the apex of the ventricle and in the cranial part of the ventricle especially most strongly on the ventral and ventrally right ventricle wall. This latter spongy structure, in the cranial part of the ventricle only, is in specimen no 1 only very feebly developed (fig. 12). In that specimen the musculature is not yet cross-striped (fig. 14, A). The septa change gradually into the ventricle wall (corticalis).

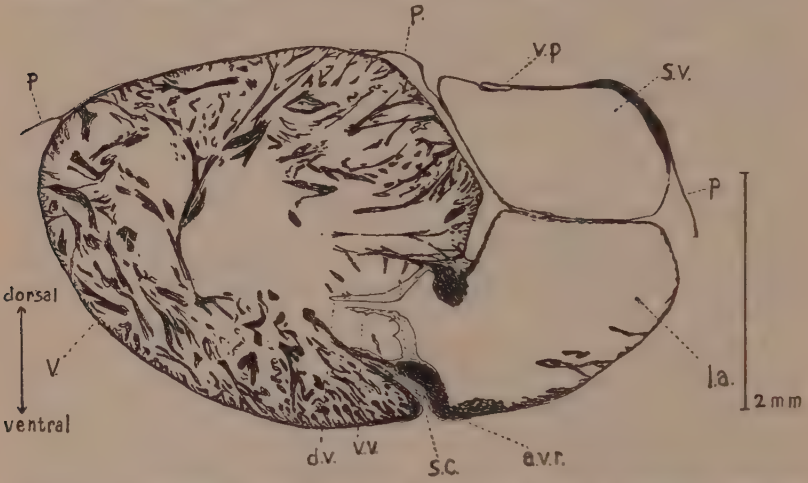

Fig. 13. Transverse section through the heart of adult *Salamandra maculosa* Laur.

v., ventricle; s.c., sulcus coronarius; a.v.r., auriculo-ventricular ring; d.v., dorsal valve; v.v., ventral valve; l.a., left atrium; s.v., sinus venosus; v.p., pulmonary vein; p., pericardium.

This ventricle wall consists in younger animals of a very thin epicardial layer, connected with the myocardium, into which the

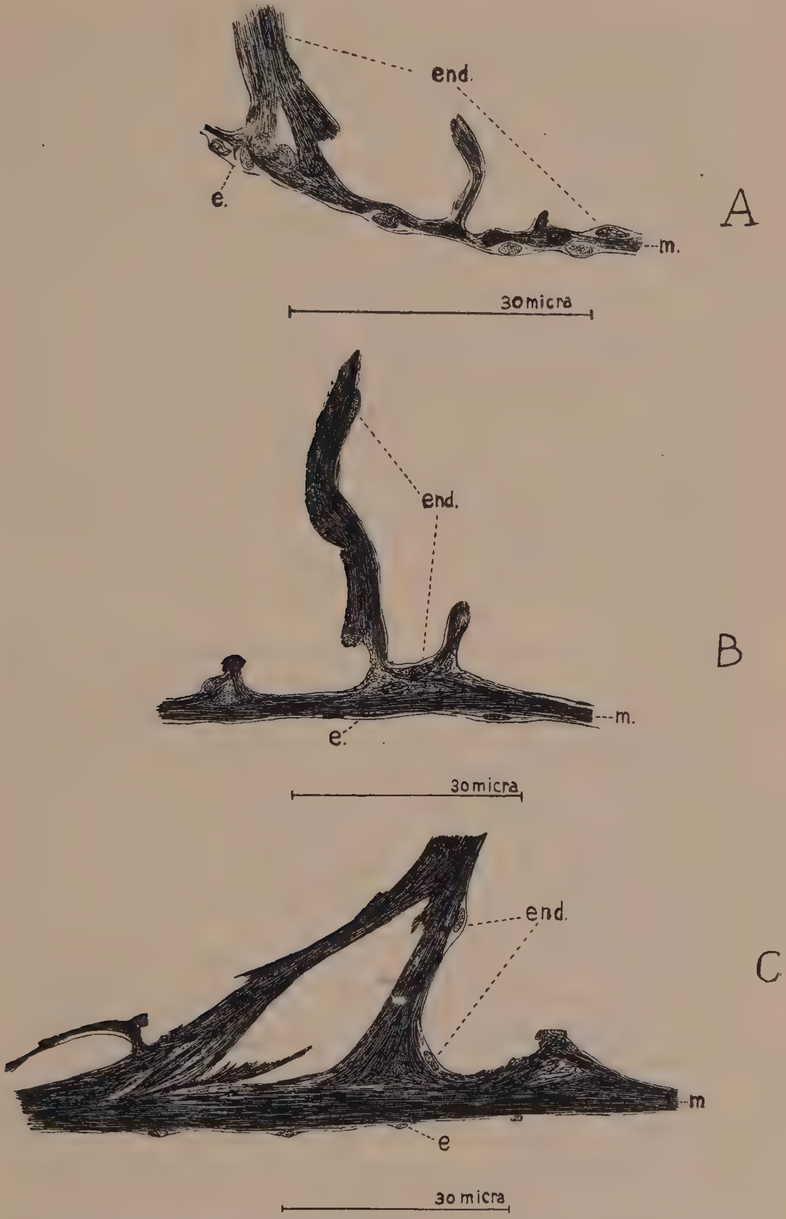

Fig. 14. Transverse sections through the wall of the ventricle of *Salamandra maculosa* Laur.

A. Before metamorphosis (no 1).
B. During metamorphosis (no 8).
C. Adult animal.
e., epicardium; end., endocardium; m., myocardium.

fibres of the septa bend (fig. 14, A). In the older animals the compactness of the myocardium increases and the fibres are cross-striped, so that in the adult animal a rather strong compact layer of muscular fibres is lying in the wall of the ventricle. Going on to the inside this compactness decreases and continues in that of the septa. In these adult animals there are on the ventricle wall numerous smaller muscular bundles arranged beside larger septa (fig. 14, C). In many places the spongy wall of the ventricle is covered with a very thin endocard layer without this layer proceeding over the whole of the wall.

A definite order of the septa and fibres is in our opinion very difficult to perceive. The muscular trabeculae bordering on the central cavity are a bit thicker and are, especially in the cranial part of the ventricle, on the ventral and dorsal sides, directed towards the ostium atrio-ventriculare. Some trabeculae round the central cavity are also directed towards the ostium arteriosum and bend into the circular musculature of the bulbus cordis.

Information regarding the vena cordis will be supplied in a later chapter.

Generally the ventricle in *Ambystoma mexicanum* Shaw seems to be less provided with muscular trabeculae and slightly smaller in respect to the atria than is the case in *Salamandra maculosa* Laur.

In the young larvae the ventricle is surrounded by a remarkably thick epicardium layer, which in neotenic animals is still present, be it in a smaller degree, especially on the right cranial and on the ventral wall of the ventricle.

Of the transformed animals, no 34 possesses a thin layer of epicardium; in both other specimens examined by us it is, however, only extremely thin.

For the rest the structure of the ventricle of the neotenic animals corresponds with that of the transformed animals.

In all animals the atrio-ventricular opening is provided with a large dorsal valve and a large ventral one. Nearly always we find a little developed endocardium ridge to the right laterally of these valves. In a few cases a small left lateral ridge may be found (nos 26 and 30).

Discussion

Owing to the extensive investigation by Benninghoff (1922) the development of the ventricle musculature and of the ventricular valves in *Triton alpestris* is accurately known. He describes (1922, p. 409) this development of the musculature as follows: "Die in der Fortsetzung des A-V-Ringes liegenden zentralen Kammertrabekel bilden sich aus leistenförmigen Erhebungen des noch einheitlichen Myokards, die in ihrer ursprünglichen Lage verharren, während sich von ihnen eine kontinuierliche Aussenschicht, die Corticalis, peripherwärts abhebt. Diese lässt von ihrer Innenfläche aus ein Netzwerk von Trabekeln entstehen und gestaltet so den inneren Aufbau und die äussere Form der Kammer." To this investigation into larvae of 4–24.2 mm we can add only very little, as our youngest larvae have a length of 23 mm. In *Salamandra maculosa* Laur. the trabeculae of the central cavity are, in our opinion, present to a much smaller extent and only to be shown in the cranial part of the ventricle.

The ventral and dorsal atrio-ventricular valves arise, according to Benninghoff, by the scooping out of the dorsal and ventral atrio-ventricular cushions. The right lateral valve is in his opinion formed later than the two large endocard cushions. According to our investigation of *Salamandra maculosa* Laur., in older larval specimens and adult animals a smaller left lateral valve can come to development.

About the ventricle and the atrio-ventricular valves of adult *Salamandra maculosa* Laur. we have more data in literature. Boas (1883) and Bruner (1900) describe in the ostium atrio-ventriculare of this species only two valves. Benninghoff (1922) examined also adult specimens of *Salamandra maculosa* and describes beside a dorsal and a ventral valve also a small right lateral valve. On the left edge Benninghoff describes a narrow edge of connective tissue connecting the bases of attachment of the dorsal and ventral valves. Züllich (1930) finds besides the dorsal and ventral valves two lateral endocard ridges to the left and right of the ostium atrio-ventriculare.

Contrary to the above, Francis's description (1934, p. 188) of *Salamandra salamandra* L. is very remarkable indeed: "in the specimen modelled, there is a hint of a double nature in this opening, since at its left end there is a shorter pair of valves partially separated from the main large pair by a fold." Körner (1938) on the other hand describes a small lateral valve and on the left side a slight endocardial ridge in the atrio-ventricular opening of *Salamandra maculosa*.

In consequence of our investigation and the data of literature we dare to conclude that in *Salamandra maculosa* Laur. there are as a rule present a larger dorsal valve and a larger ventral one and a smaller right lateral valve. A fourth, left lateral valve may come to development, or is else present as an endocardial ridge in adult animals.

Boas (1883) describes for *Siredon* the presence of a large dorsal valve and a large ventral one in the atrio-ventricular opening. Körner (1938) finds in one neotenic specimen of *Ambystoma mexicanum* and one transformed specimen a large left dorsal valve, a large right ventral valve and a smaller right dorsal one. Moreover, however, there is always a small ridge to the left ventrally.

For *Ambystoma mexicanum* Shaw we generally find a large dorsal valve and a large ventral one, and a small right lateral valve usually not containing a hollowness. Very seldom we found the fourth left lateral ridge to be present.

In *Salamandra perspicillata* (Cords, 1924) and *Cryptobranchus japonicus* (Osawa, 1902) muscular elements are described in the chordae tendineae. In *Salamandra maculosa* Laur. and *Ambystoma mexicanum* Shaw we cannot detect any, neither could Benninghoff (1922).

The arrangement of the musculature of the ventricle of *Salamandra maculosa* has already been fully described by Züllich (1930). We are, however, of opinion that this musculature is not wholly covered by an endocardial layer, as he stated.

Bulbus cordis

Own investigation

The bulbus cordis originates in the most cranial part of the ventricle, as has been described in the section dealing with the ventricle. Cranially in respect to the ostium arteriosum, in the caudal part of the bulbus cordis, this bulbus has a bend from caudally right and dorsal to cranially left and ventral. This bend is present already in the youngest specimen, but is also perceivable in all the younger larval specimens (fig. 15, no 3). Already in the larval specimens during metamorphosis the curve of this bend is slighter.

Cranially from this bend the bulbus cordis runs across the right ventral wall of the atria slightly from caudally right to

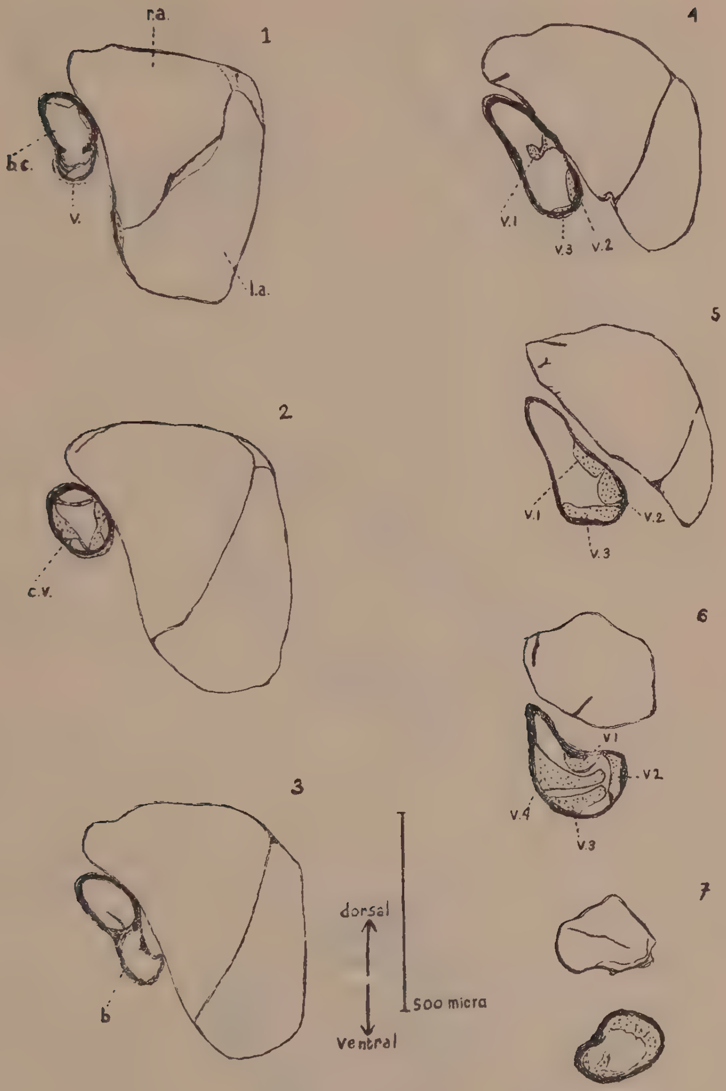

Fig. 15. Transverse sections through the cranial part of the larval heart of *Salamandra maculosa* Laur. (no 1).
1 to 7 = caudal to cranial.
r.a., right atrium; l.a., left atrium; v., ventricle; b.c., bulbus cordis; c.v., caudal valves; b., bend in the caudal part of the bulbus cordis; v.1, v.2, v.3, v.4, cranial valves.

cranially left. Not only owing to this obliquity, but also through its real shape the sections of the bulbus cordis are oval halfway the bulbus, its horizontal axis lying from dorsally right to ventrally left.

Especially in the younger larval specimens (nos 1–4) the cranial part of the bulbus cordis has a slight bend, so that its direction from caudally right to cranially left is changed into caudally to cranially (fig. 15). In this bend the bulbus cordis is at the same time narrowed and alters headwards into the truncus arteriosus. This latter bend, which is clearly developed in young larvae especially, is hardly present in older larvae and adult animals. The specimens nos 16 and 17, however, form an exception; both of them clearly possess the bend described.

In the caudal part of the bulbus cordis, at the alteration of the ventricle into the bulbus cordis, there are three pocket valves with their concavities cranially. Already in the youngest specimen examined these concavities are present (fig. 15, no 2), gradually growing larger in the older specimens (fig. 16, no 1). The valves are nearly always distributed on the inner wall of the bulbus cordis in the same manner. One large valve is dorsally and a bit to the right, another large valve extends on the left ventral wall of the bulbus cordis, while a third somewhat smaller valve is situated on the right ventral wall (fig. 15 and 16).

Between the cranial bases of attachment of the two ventral valves there is mostly some space left, whereas the cranial bases of attachment of the dorsal and lateral valves are situated directly against each other (fig. 16, no 1). These last points of attachment are often covered with thicker endocardium layers, so that the valves are more or less connected with one another. This is especially the case between the dorsal and ventral left valves.

Deviations from the situation described are more than once found. So e.g. the specimens nos 6 and 15 of the larvae and 18 and 19 in the adult animals possess a fourth very small valve, situated between the dorsal and left ventral ones described above, where especially in the larvae thicker endocardium layers are found. By this increase in the number of valves the arrangement may change a little.

The valves always possess a larger size laterally than in caudal-cranial direction. In young larval specimens the valves consist in a homogeneous mass of connective tissue, in which in older

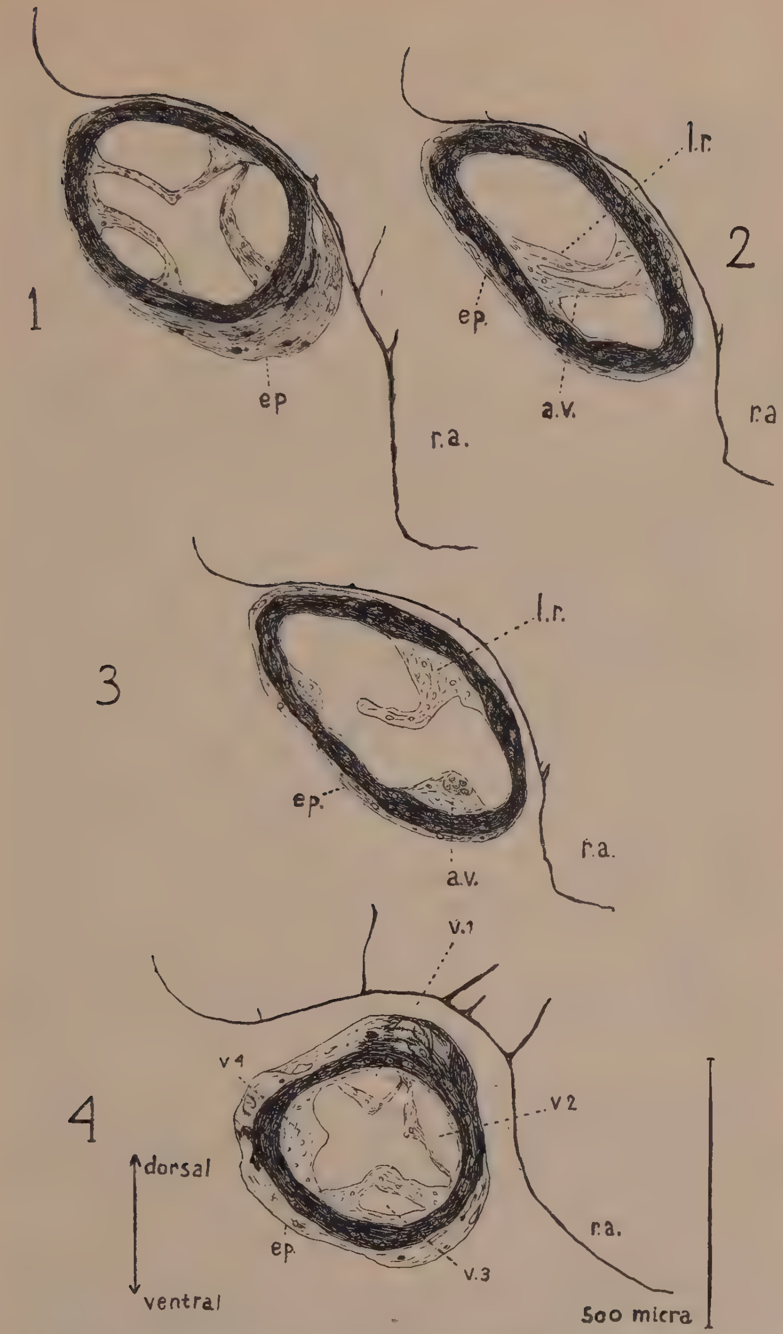

Fig. 16. Transverse sections through the bulbus cordis of a larva of *Salamandra maculosa* Laur. (no 8).
1 to 4 = caudal to cranial.
r.a., right atrium; ep.; epicardium; l.r., longitudinal ridge; a.v., accessory valve; v.1, v.2, v.3, v.4, cranial valves.

larvae and in adult animals fibres appear. In older larvae and adult animals the cranial bases of attachment are very thin, or even reduced to some finer trabeculae only. Muscular elements are not present here. In some cases the trabeculae of two valves are connected with each other. Trabeculae from the concave walls of the valves to the bulbus wall are very rare and only present in the neighbourhood of the bases of attachment of the valves in adult animals.

In the right part of the caudal wall of the bend of the bulbus we always find an endocardium thickening continuing cranially in the bulbus as a bridge between the dorsal left and ventral right bulbus walls (fig. 15, no 3 and 16, no 2). Some sections cranialwards from its caudal basis the right ventral attachment of this bridge detaches itself from the right ventral bulbus wall, so that slightly more cranially a ridge protrudes into the bulbus cavity, which is attached to the left dorsal wall of the bulbus. This is the so-called longitudinal ridge or spiral valve. In its course from tailward to headward the base of attachment of this ridge to the bulbus wall runs a little from dorsally left to dorsally, so that this line may be considered as the axis round which the bulbus is twisted. In general the height of the ridge declines from caudally to cranially, to increase again in its most cranial part. The average height of the ridge surpasses half of the diameter of the bulbus lumen. Its most cranial part is always provided with a much broader base of attachment than its caudal part. This cranial part is in the youngest larvae (nos 1 and 2) wholly massive and does not possess a concavity (fig. 15, nos 5 and 6). In our specimen no 3 this concavity is present, so that in the successive stages it changes into the cranial bulbus valve called no 1 by most authors, which term we shall also adopt.

In the youngest larval specimens (nos 1 and 2) there are in the cranial part of the bulbus cordis, besides the ridge described above, three other ridges arranged on the rest of the bulbus wall, which extend much less caudally (fig. 15 and 16). All the ridges fill up nearly the whole cranial part of the bulbus cavity. In specimens older than our specimen no 2 all these ridges obtain an excavation opening up cranially, which may have originated by scooping out, as in the young specimens the bulbus cordis was entirely filled up with these endocardium ridges.

The general arrangement of these valves is as follows; valve no 1, the cranial continuance of the longitudinal ridge, is comparatively very large and situated dorsally; valve no 2 is slightly smaller and extends to the left and a little dorsally; valve no 3 is very large again and is arranged ventrally; the smaller valve no 4 is lying dorsally and a little to the right (fig. 15 and 16).

These valves possess in general a larger caudally-cranial size than they do in lateral direction. In the younger specimens the valves are built up from homogeneous connective tissue. In older larvae and adult animals this connective tissue is provided with fibres. The cranial parts of the bases of attachment are very thin and even broken up into trabeculae..

In many cases the free margins of two adjacent valves are connected with each other by these trabeculae. For the rest, trabeculae from the inner walls of the valves to the bulbus wall are very rare. Muscular elements in this structure are not perceivable. In one of the adult specimens there is in valve no 4 in its caudal base a couple of ball-shaped cartilaginous bodies. In another adult specimen (no 22) we find a ball-shaped cartilaginous body in the caudal base of the longitudinal ridge. This cartilage always has a hyaline structure.

To the regular arrangement of the cranial bulbus valves described above we find few exceptions only. It is true, we meet with remainders of valves in this part in the shape of endocardium knobs on the bulbus wall. So e.g. in specimens nos 8 and 13 there is caudally to the basis of valve no 3 and not attached to it an endocardium thickening of the bulbus wall (fig. 16, no 3). This thickening has in specimen no 8 a small ball-shaped cartilaginous body. In one of the adult specimens (no 22) we find to the right of the caudal base of the longitudinal ridge an endocard thickening on the bulbus wall containing a small cartilaginous body. We find in specimens nos 7 and 9 a small side-valve to valve no 4 arranged dorsally in respect to this valve and connected with it. Also we sometimes find in the cranial part of valve no 1 a side-valve lying dorsally and cranially connected with the excavation of valve no 1.

In a great many larvae a second endocardium bridge is met with to the left of the caudal base of the longitudinal ridge between the right ventral and left dorsal walls of the bulbus (fig. 16, no 2). This bridge is cranially attached to the ventral right wall only, to disappear into it gradually in cranial direction.

The bulbus wall clearly consists of three layers: the epicardium, the myocardium and the endocardium. The epicardium layer is in the youngest specimens remarkably thick, especially on the ventral side of the caudal part of the bulbus. In these young larvae the myocardium consists in undifferentiated muscular elements. The inner wall of the bulbus, the endocardium, is, not counting the valves, clearly present as a continual layer, especially in the caudal part of the bulbus. This endocardium is least perceivable halfway the bulbus. In specimens older than our specimen no 3 the muscular fibres of the myocardium show cross-striping. In some of these specimens there are also perceivable small fissures between the fibres. In the older larvae and in adult animals the course of the muscular fibres is, in transverse sections only, difficult to follow. In the caudal part of the bulbus cordis, cranially to the ostium arteriosum, these fibres are arranged circularly, which is also the case in the most cranial part of the bulbus. Halfway the bulbus the direction of the fibres is most difficult to perceive, partly because of the presence of the bend, partly owing to the course of the bulbus cordis. Halfway the bulbus there are certainly fibres present, which are circularly arranged round the bulbus cavity. Outside and inside this layer, however, there seem to us also longitudinal bands to be present.

In the cranial part of the bulbus in older larvae and adult animals, cranially from the free margin of the cranial valves, there is a thin layer of smooth muscular fibres on the inner wall of the bulbus, separated from the cross-striped fibres of the outer wall by fibrous connective tissue. These smooth muscular fibres belong to the truncus arteriosus wall. Owing to the slight differentiation in young specimens the development of this relation is difficult to perceive. When discussing the truncus arteriosus we shall refer to this.

In older larvae and adult animals the epicardium is less thick than in younger larvae. In these older specimens it contains in the caudal part of the bulbus bloodvessels entering into the myocardium and vascularizing the muscular mass slightly. We shall deal with this later on again.

In the bulbus cordis of *Ambystoma mexicanum* Shaw the caudal bend is very little developed in the young larvae (nos 23, 24, 25 and 26). In the neotenic animals and the transformed animals on the other hand the bend is much more clearly perceptible. So this situation is the reverse of that in *Salamandra maculosa* Laur.

The cranial bulbus bend on the change of the bulbus cordis into the truncus arteriosus is hardly perceivable in the younger larvae of *Ambystoma mexicanum* Shaw, but much more distinctly perceivable in all older animals before and after metamorphosis. So this situation, too, appears to be the reverse of that of *Salamandra maculosa* Laur.

In general three valves were found in the caudal part of the bulbus cordis, in about the same arrangement as in *Salamandra maculosa* Laur. Already in the young specimens these valves contain excavations.

Some animals clearly possess four valves, and it is remarkably the young larval animals that show this relation. However, we do not presume this to be a larval characteristic.

Also in no 27 a fourth endocardium knob is present between the two caudal valves on the ventral wall of the bulbus cordis. In no 30 we find a fourth small valve on the ventral wall. In these cases the valves do not lie on their normal places.

As the caudal bend is very slightly developed the longitudinal ridge appears to arise from the left ventral bulbus wall in the young larvae. More cranially this ridge extends on the left and left dorsal walls of the bulbus cordis. In the neotenic and transformed animals the position of the longitudinal ridge is the same as in *Salamandra maculosa* Laur.

In general the longitudinal ridge is broader and higher in transverse sections than in *Salamandra maculosa* Laur.

Invariably four cranial valves are found in the bulbus cordis in the same arrangement as in *Salamandra maculosa* Laur. Already in the youngest animal these valves contain excavations.

In no 25 an endocardium cushion is present on the right wall of the bulbus cordis opposite the free margin of the longitudinal ridge.

In nos 26 and 35 a small endocardium knob is found dorsally of the caudal part of the longitudinal ridge. In no 29 a small knob is present between valves nos 3 and 4.

Cartilaginous bodies are not found in the cranial valves.

The whole of the bulbus cordis, but especially its caudal part, is surrounded by thick epicard layers. This epicardium lies especially on the ventral wall of the bulbus cordis and extends also in older animals far cranially.

Discussion

After Brücke (1852) and Leydig (1853) it is especially Boas (1882), who has accurately examined this part of the heart, called by him conus arteriosus, in adult *Salamandra*. After Boas had stated the homology of this organ with the conus arteriosus (Gegenbaur, 1866) of Ganoidae and Selachii the name bulbus cordis has been given to this part of the heart by Langer (1894).

Langer (1894) examined two larval specimens of *Salamandra maculosa* of 2.2 and 2.9 cm. In later literature we find information about the bulbus cordis of adult *Salamandra maculosa* in Bruner (1900), Züllich (1930), Francis (1934) and Körner (1938).

Boas (1882) thought that the conus arteriosus of the Amphibia is to be derived from that of *Ceratodus*. This conus of *Ceratodus* is described by him (1882, p. 511) as follows: "Der Conus war spiralig gedreht and zwar so, dass die Achse der Spirale eine in der Wand des Conus liegende Linie war; die Achse war dann ungefähr in ihrer Mitte wie geknickt, was natürlich auch auf die Gestalt des ganzen Conus Einfluss hatte. Längs der Achse fanden wir im Conus eine Reihe von acht Klappen, von welchen die sechs hinteren stark ins Lumen einsprangen; die ganze Reihe nennen wir die Longitudinalfalte. Im vordern Ende des Conus fanden wir zwei Querreihen von Taschenklappen, vier in jeder; zwei dieser acht Klappen gehörten zugleich zur Longitudinalfalte. In der Mitte des Conus war eine Partie, an der keine Querreihen von Klappen sich fanden; im hinteren Ende desselben trafen wir wieder einige solche an."

Boas (1882, p. 489) describes the bulbus cordis of *Salamandra* as a "kurzes, spiraliges Rohr". Beside the internal relation, which is to be discussed later on, Boas bases on the twisted shape the comparison of the conus arteriosus of Urodela with the conus of *Ceratodus*. Boas thinks it a difficulty in this comparison that the bend is lacking in the conus of *Salamandra*. As Langer (1894) already describes, this bend is also present in the bulbus cordis of *Salamandra* larvae, and can be clearly seen in all the larvae of *Salamandra maculosa* Laur. which were examined by us, but especially in the youngest specimens.

Körner (1938) expresses the possibility that the spiral shape should have arisen secondarily, as in a newly metamorphosed specimen of *Pleurodeles waltlii* no spiral shape is present, whereas in the adult animals of this species a clear spiral occurs. According to our investigation the twisted shape is more clearly perceivable in the youngest larval specimens of *Salamandra maculosa* Laur. than in older larvae and adult animals.

Although in young larvae of *Ambystoma mexicanum* Shaw the twisted shape is much less developed than in the neotenic and transformed animals, we are yet of opinion that this twisted shape is to be considered original, as it is visible in young larvae of *Ambystoma mexicanum* Shaw and clearly perceivable in the youngest larval specimens of *Salamandra maculosa* Laur.

LANGER (1894) describes three endocardium ridges in the caudal part of the bulbus cordis in a larva of *Salamandra maculosa* of 2.3 cm. Only in a larva of 2.9 cm examined by him the dorsal and ventral left ridges possess an excavation. In the youngest larva examined by us (22 mm) all valves in the caudal part of the bulbus have already come to development. LANGER's opinion that these valves originate by scooping out of the endocardium ridges we can support as far as it is perceivable and provable.

The descriptions of the number and arrangement of the caudal bulbus valves in adult *Salamandra maculosa* Laur. are rather different in literature. BOAS (1882) found three, sometimes four, valves. ZÜLLICH (1930) describes three caudal valves and points out that variance was not perceived by him. BRUNER's (1900) and FRANCIS's (1934) descriptions agree with this as to the number of valves found. KÖRNER (1938) examined two specimens of *Salamandra maculosa* and describes four caudal valves. In connection with our own investigation and seeing the data of literature we dare to conclude that in *Salamandra maculosa* Laur. in general, the caudal part of the bulbus cordis is provided with a large dorsal right valve, a large ventral left valve and a slightly smaller ventral right valve. In the larvae and especially in the adult animals a smaller dorsal left valve may be found in the place where also thicker endocardium layers may be situated. Through the development of this fourth valve the arrangement of the three first mentioned valves may undergo some change.

For *Siredon* BOAS (1882) found in the two specimens examined by him three or four valves in the caudal part of the bulbus cordis. In *Amblystoma* he found three valves in this part of the bulbus cordis. KÖRNER (1938) gives for two specimens of the neotenic axolotl four valves in the caudal part of the bulbus cordis. In one of these specimens the right ventral valve was rudimentary.

Generally we found three valves in the caudal part of the bulbus cordis of *Ambystoma mexicanum* Shaw, although in young larvae a fourth valve was present. Yet we do not think this to be a larval characteristic. In adult animals a fourth valve may appear or be present as an endocard knob on the bulbus wall.

Boas (1882) describes four cranial valves in the bulbus cordis, of *Salamandra*, of which no 1 changes caudally into the longitudinal ridge. He describes this (1882, p. 490) as follows: "Die Longitudinalfalte . . . läuft an der dorsalen Wand des Conus von vorn rechts bis hinten links, ja sogar auf die ventrale Fläche herum; ihre Anheftungslinie ist fast gerade, und bildet die Achse der Spirale." This ventral attachment of the longitudinal ridge was never perceived by us and in our opinion the spiral course of this ridge is represented too strongly by Boas.

Langer (1894) describes four ridges in the cranial part of the bulbus in the larvae of *Salamandra maculosa*. Judging from his figures valve (ridge) no 1 has been placed too far to the right in the cranial part of the bulbus as compared with our data. Hereby this spiral valve seems to us to be represented too strongly spiral-shaped. Wirtinger (1937), too, represents the longitudinal ridge too spiral-shaped.

In the larvae of *Salamandra maculosa* Laur. examined by us the excavations in these cranial ridges are present from specimen no 3 (36 mm) onward, while Langer comes upon these excavations in a larva of 2.9 cm already.

Bruner (1900), Züllich (1930), Francis (1934) and Körner (1938) describe four valves in the cranial part of the bulbus in adult specimens of *Salamandra maculosa*. The arrangement of these valves is not always stated in the same way, which is quite comprehensible seeing the subjectivity of the determination of place.

In the cranial part of the bulbus cordis of *Siredon* and *Amblystoma* Boas (1882) found four valves of which no 2 was smaller. Körner (1938) describes for *Ambystoma mexicanum* the same arrangement of four cranial bulbus valves as we ourselves have done.

Körner (1938), however, describes for one specimen of *Salamandra maculosa* and for one specimen of *Ambystoma mexicanum* a connection of the caudal part of the longitudinal ridge with one of the ventral caudal bulbus valves, a connection nowhere seen by us neither mentioned in other literature.

A minute description of the valves is found in Boas (1882) and Züllich (1930). From the descriptions of the cranial bulbus valves of *Salamandra maculosa* by BOAS and ZÜLLICH we get the impression, and from ZÜLLICH's figures it is obvious, that these authors found cartilaginous bodies in each of the cranial bulbus valves. We found this cartilage only in two of the adult specimens of *Salamandra maculosa* Laur., in one case in valve no 1, in the other in valve no 4. KÖRNER (1938), too, finds in other species of Urodela – *Salamandra atra*, *Molge cristata* and *Molge pyrrhogastra* – these bodies in the right valve. Also in *Euproctus asper* in the right and left valves, in *Pleurodeles waltlii* in the right, left and ventral valves and in *Hynobius naevius* in the spiral valve. KÖRNER thinks that they occur mostly in the right valve. His surmise that this cartilage should be dependent on old age seems to us not correct, as in larva no 8 examined by us this cartilage is already present, be it in a remainder of a valve. MATUMOTO (1938), too, found this cartilage already present in the septum bulbi of two specimens of *Hynobius leechii* Boulenger – seven days and two weeks after metamorphosis respectively.

In comparison with the conus of *Ceratodus* BOAS (1882) says that in the conus of *Salamandra* only the most cranial and most caudal transverse rows of valves are left, while also the seven most cranial valves of the longitudinal row remain and grow together into one ridge. In *Ceratodus* there is in the same transverse plane as the bend the third valve (counted from cranially; BOAS, 1880) of the longitudinal row. Thus LANGER (1894) rightly pointed out that the longitudinal ridge of *Salamandra maculosa* only contains the three most cranial valves of the longitudinal row of *Ceratodus*. As has been described by us, the course of the longitudinal ridge is not so spiral-shaped over the bulbus wall as was described by BOAS (1882) and LANGER (1894). We are of opinion that this agrees with the fact that this ridge only covers the three most cranial valves of the row.

It is not impossible that the rests of valves in the cranial part of the bulbus, as described by us, are rests of the second transverse row of valves in the cranial part of the conus of *Ceratodus*.

NOBLE (1925) found accessory valves in *Notophthalmus torosus*, KÖRNER (1938) found them in *Hynobius keyserlingii*, *Molge vulgaris*, *Molge cristata*, *Pleurodeles poireti* and *Ambystoma mexicanum*.

The difference between the bulbus cordis (conus arteriosus) and a truncus arteriosus rests on a difference in wall structure, as has been pointed out first by BOAS (1882). BOAS (p. 490) describes the fibres of the bulbus cordis as being "quergestreifte gewöhnlich an beiden Enden zerklüftete Muskelzellen". The splitting of these muscular fibres could not be clearly seen by us.

Already Greil (1903) and Körner (1938) describe on the inside of the cranial part of the bulbus a layer of smooth muscular fibres. Both describe the cross-striped muscular layer of the bulbus cordis extending over the outside of the truncus arteriosus. This relation we shall discuss in the following chapter.

IV. THE TRUNCUS ARTERIOSUS AND THE ARTERIAL ARCHES

Truncus arteriosus

Own investigation

The bulbus cordis extends cranially into the truncus arteriosus. This truncus lies about caudo-cranially and rather in the median plane of the body. Caudally the cavity of the truncus consists of an undivided space, which is cranially divided into eight canals, the root-vessels of the arterial arches, by the appearance of septa in the cavity. The transverse section is in the caudal part of the truncus in general a little oval-shaped, the axis being horizontal. In its cranial part the transverse section is more triangular, one of its sides lying dorsally, especially because of the canals being arranged laterally and ventrally round a lymph heart (fig. 17). The truncus widens going from caudal to cranial direction. The caudal part of the truncus splits into the arterial arches, each of which originates separately at the truncus.

Whereas the entire truncus lies in the youngest larvae already within the pericardium, the arterial arches are situated outside the pericardium (fig. 17). Pericardium and lymph space will be dealt with in a separate chapter.

As has been discussed in one of the foregoing parts, the truncus moves caudally during the development. It appeared from table IV and fig. 3 that the distance between the backs of the occipital condyles and the front of the bifurcation of the carotids during the development shown by specimens nos 1, 2 and 3 shows an increase in proportion to the growth of the body. During the development shown by specimens nos 4, 5 and 6 this distance shows no increase in respect of the growth of the body. In specimens older than no 6 a definite caudal movement is to be perceived.

The muscular layer of the bulbus cordis extends as a continuous

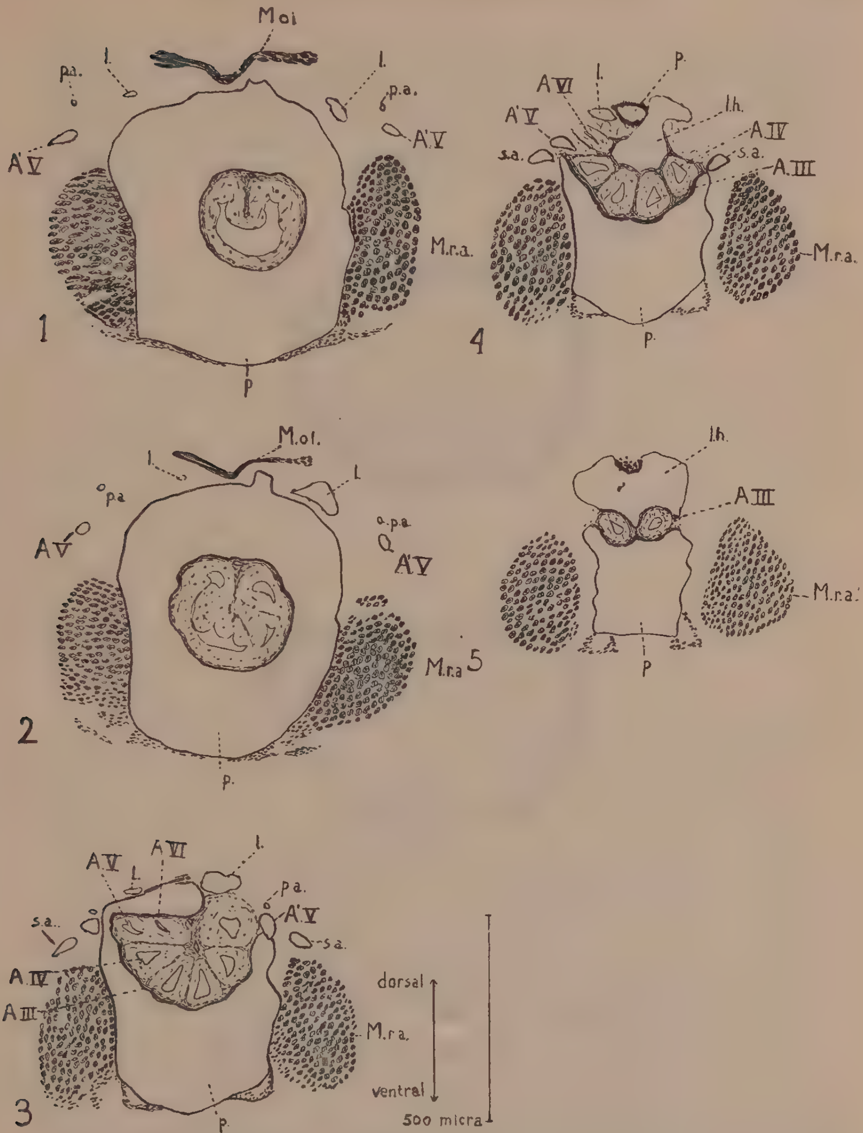

Fig. 17. Transverse sections through the pericardium and the truncus arteriosus of a larva of *Salamandra maculosa* Laur. (no 1).
1 to 5 = caudal to cranial.

p., pericardium cavity; M.r.a., musculus rectus abdominis; M.o.i., musculus obliquus internus; l., lymphatic vessel; l.h., lymph heart; c.a., carotid arch; s.a., systemic arch; A′.V, "third" arch; p.a., pulmonary arch; A.III, IV, V and VI, root-vessels of the arterial arches.

sheath over the whole of the truncus arteriosus (fig. 17, 18 and 19). This sheath ends on the truncus wall on the plane of intersection of the pericardium and the truncus wall (fig. 17, no 3). The epicardium of the bulbus cordis, too, extends as a thin layer over the outside of the above sheath. In the youngest specimens a differentiation in the fibres of this muscle sheath is not yet perceivable. In specimens older than no 3 the fibres show cross-striping. In older larvae the arrangement of these fibres in the caudal part of the truncus seems to us to be circular; in the cranial part the fibres are arranged from caudo-laterally left and right to cranially-dorsally and ventrally median. Especially

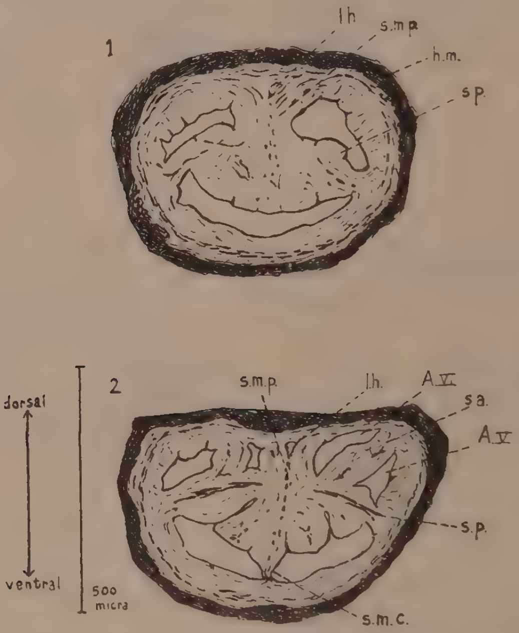

Fig. 18. Transverse sections through the truncus arteriosus of a young specimen of *Salamandra maculosa* Laur. (no. 14).
1 = caudal; 2 = cranial.
A.V and VI, root-vessels of the arterial arches; s.m.p., septum medianum pulmonale; s.a., septum accessorium; s.p., septum principale trunci; s.m.c., septum medianum caroticum; l.h., lymph heart; h.m., heart muscle sheath.

in the dorsal-median line of the truncus the fibres form a stronger muscular band. These dorsal and ventral truncus musculatures are cranially from the carotid bifurcation connected with each other.

Within the sheath of cross-striped musculature lies the truncus arteriosus wall. In the youngest larvae this truncus wall consists of a layer of fibrous connective tissue lying directly against the cross-striped musculature, while within this fibrous connective tissue layer a homogeneous layer of connective tissue is found (fig. 17).

In consequence of this structure the whole of the truncus wall is, cranially of the bulbus valves, much thicker than the wall of the bulbus cordis. Only in the older larvae and adult animals there are, cranially from the free margins of the bulbus valves, smooth muscular elements in the fibrous connective tissue layer. When the larvae grow older the homogeneous connective tissue layer gets much thinner and the truncus wall, in which smooth muscular fibres are clearly perceivable, is separated from the outer cross-striped muscular sheath by a meshy connective tissue (fig. 18 and 19).

The unsplit truncus is already in the youngest larvae very short. Cranially there arises on its dorsal wall a ridge, the septum medianum (fig. 17). The end of this ridge, protruding into the truncus cavity, is strongly thickened in the larval specimens nos 1–6 by homogeneous connective tissue (fig. 17). The fibrous connective tissue penetrates into the middle of the ridge. Following the margin of the ridge cranially the other septa appear in the truncus originating from the margin of the ridge and extending till they reach the truncus wall. These septa are also in the youngest larvae covered with a thick homogeneous connective tissue layer (fig. 17 and 18). Into this homogeneous connective tissue layer penetrates the fibrous layer. In older larvae and adult animals there appear in these septa smooth muscular fibres, while the homogeneous connective tissue has disappeared. These muscular fibres are in general arranged in two layers: one outer layer round the entire truncus wall and an inner one arranged round each of the cavities of the root-vessels (fig. 19). The caudal extension of these septa is different. In general a horizontal wall extends most caudally – the septum principale trunci – so that a dorsal and a ventral part can be distinguished in the truncus cavity. In all the specimens three septa extend in the ventral truncus space slightly less caudally than the horizontal septum: one septum medianum caroticum, which divides this ventral space into a left half and a right one, and two septa attached to the right and left ventral-lateral truncus walls (septa carotico-aortica) (fig. 18 and 19). In adult animals the septum medianum caroticum extends more caudally than the septa carotico-aortica. Hereby the ventral truncus cavity is divided into four root-vessels of the arterial arches (A. III, the root-vessels of the carotids and A. IV, the root-vessels of the aorta). In the dorsal part of the truncus arise two septa attached to the dorsal lateral truncus walls: the septa accessoria, so that here, too, four root-vessels of the arterial arches are formed (two median vessels of the pulmonalis, A. VI, and two lateral vessels of the arterial arches, A. V) (fig. 18 and 19). In the specimens nos 1 and 2 these latter septa (s. accessoria) extend very little caudally (fig. 17). In older larvae and adult animals they extend much more caudally in respect to the other septa (fig. 18). From this it appears that the formation of these may take place through

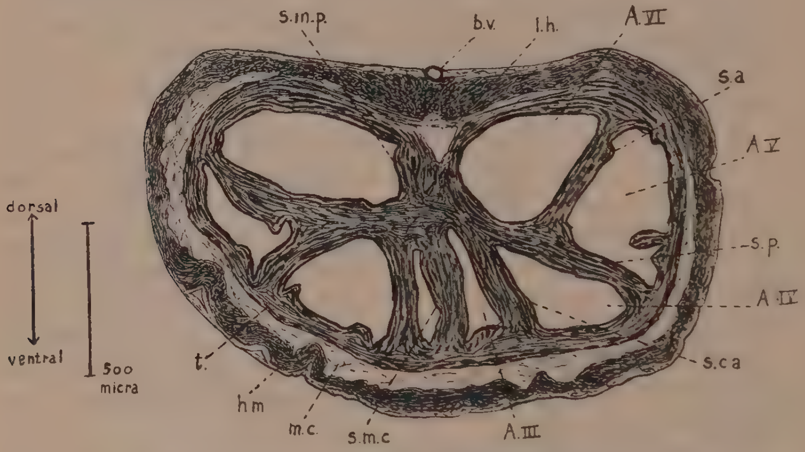

Fig. 19. Transverse section through the truncus arteriosus of an adult *Salamandra maculosa* Laur. (no 18).
A.III, IV, V and VI, root-vessels of the arterial arches; s.m.p., septum medianum pulmonale; s.a., septum accessorium; s.p., septum principale trunci; s.c.a., septum carotico-aorticum; s.m.c., septum medianum caroticum; t., truncus wall; h.m., heart muscular sheath; m.c., meshy connective tissue; b.v., bloodvessel (artery); l.h., lymph heart.

caudal lengthening of the septa. In all specimens the septum accessorium is present.

In some cases the arterial arches V are lacking (see "Arterial arches"). In all these cases, however, the root-vessels of these arches are present in the truncus arteriosus but end cranially blind.

In the centre of the median septum lies the caudal base of the lymph heart, laterally and ventrally of which the root-vessels are arranged. The caudal base of the entire lymph heart is surrounded by the tissue of the truncus wall. In younger larvae the caudal base of the lymph heart seems less caudal in respect to the bifurcation point of the arterial arches than is the case in older larvae. In consequence of this the most cranial part of the truncus seems to us to have also arisen from the growing together of the arterial arches. In the caudal part of the truncus the septa seem to us to lengthen by caudal growth.

The diameter of the vessels is very different. In young specimens the root-vessels of the pulmonalis are very narrow, growing much wider in older specimens (specimens older than no 6). In younger larvae the root-vessels of the arterial arches V are wider than those of arterial arches IV. In older larvae and adult animals these relations are reversed.

In the dorsal wall of the truncus a bloodvessel is found in caudal-cranial direction in older larvae and adult animals, which will be discussed later on.

The cavity of the truncus arteriosus in *Ambystoma mexicanum* Shaw is divided cranialward into six or eight canals (see "Arterial arches"). In all specimens slightly more cranially of the free margins of the cranial bulbus valves a ridge is present on the dorsal wall of the truncus arteriosus. The free margin of this ridge is in the transverse section thickened in the shape of a bulb.

Cranialward arise the truncus septa from this bulb-shaped ridge, so that usually first the septum medianum caroticum reaches the ventral wall of the truncus arteriosus. Slightly more cranially of this the septum carotico-aorticum reaches the lateral ventral wall of the truncus arteriosus. Again cranially of this the septum principale trunci reaches the lateral wall of the truncus arteriosus. Most cranially appears the septum accessorium. In the specimens nos 26, 31, 32, 33 and 38 this septum is not present, and the truncus arteriosus has only six canals.

In older animals this arrangement may be slightly modified by the septum principale trunci extending most caudally.

The septa contain in the young larvae nos 25 and 26 a homogeneous connective tissue layer. The larvae nos 23 and 24 have this to a much lesser extent. In the neotenic animals this connective tissue is still present in no 30. In the transformed animals the connective tissue has disappeared; the septa, however, are much thicker than in *Salamandra maculosa* Laur.

The diameter of the canals is very different. As a rule the root-vessels of the pulmonary arches are very narrow in young larvae and neotenic animals. The root-vessels of the "third" arches get thinner as compared with those of the systemic arches (A. IV) during development.

Discussion

In ZÜLLICH's (1930) description and figures of the truncus arteriosus in adult *Salamandra maculosa* the truncus in its external appearance shows a caudal undivided part, splitting up cranially into a left and a right truncus. This shape, representing the general situation in Anura, has never been perceived by us in *Salamandra maculosa* Laur. In none of the specimens examined by us, did we find a right and a left truncus externally separated from each other (see "Arterial arches").

About the building up of the truncus arteriosus there are two theories. According to BOAS (1882) the unsplit cavity belongs to the part agreeing with the truncus of fishes, while the split part of the cavity is built up from the arterial arches grown together. This situation is the same as that of *Ceratodus*. By smooth muscular fibres the truncus is distinguished from the bulbus cordis. The outer cross-striped muscular sheath of the truncus BOAS seems to have overlooked. BOAS's opinion about the building up of the truncus is also found in ZÜLLICH (1930).

According to GREIL (1903 A and B), whose theory is confirmed by HOCHSTETTER (1906) and KÖRNER (1938), the distinction between an undivided and a divided truncus is not correct on principal grounds, but the divided part should have arisen from the caudal growth of the walls between the bifurcation points of the arterial arches into an originally wholly undivided truncus. Both theories seem to us difficult to prove. Our own research, too, seems to be not capable of doing so. Only the fact that the caudal margins of the septa accessoria end more cranially in the younger specimens than in the older ones in respect to the other septa would be in favour of GREIL's theory.

The thickening of connective tissue on the septa as found by us in the larvae, was already described by BOAS (1882) for *Siren*, *Siredon* and *Amblystoma;* by KÖRNER (1938) for *Ambystoma mexicanum* (two of which non-metamorphosed, and one metamorphosed), *Ambystoma opacum*, and for young specimens of *Pleurodeles waltlii.*

Although in two very young larvae of *Ambystoma mexicanum* Shaw the tissue thickenings on the truncus septa are lacking, they are present in two less young larvae. In neotenic specimens the thickenings are slighter, although still present. In the transformed specimens the thickenings are almost completely lacking.

Also judging from the fact that in *Salamandra maculosa* Laur. the young larvae possess these thickenings, whereas the adult specimens do not, these thickenings seem to us, contrary to BOAS (1882), larval characteristics.

The cross-striped layer of muscular fibres round the truncus arteriosus has first been described by GREIL (1903 A) in *Salamandra atra*. According to GREIL this layer drives the lymph to the lymph heart by systolic contraction. Without further explanation BENNINGHOFF (1933, p. 493) says: "Es ist aber offenbar die Herzmuskulatur am Trunkus des Salamanders dem Lymphherzen zugeordnet und als eine besondere Spezialisierung aufzufassen."

KÖRNER (1938) found this layer of muscular fibres in all the Urodela he examined. For *Proteus anguineus* KÖRNER does not find a lymph heart, but does find a cardiac layer of muscular fibres round the truncus. About the development of this layer GREIL (1903 A, p. 104) writes as follows: ". . . ich (will) nur ganz kurz hervorheben, dass dieselbe zugleich und in continuo mit dem Myocard aus der Splanchnopleura hervorgeht, welche den gegen den Herzschlauch zu, also intrapericardial sich verlängernden Truncus arteriosus ebenso umgibt, wie das Epithelrohr des Herzens selbst". Seeing these facts, but also seeing the importance from a point of view of comparative anatomy, it seems to us very desirable to subject the judging of this muscular layer to a more detailed examination.

The caudal extension of the septa is by various authors represented differently for adult specimens of *Salamandra maculosa*

Laur. In all their data the dorsal part of the septum medianum pulmonale extends most caudally. Slightly less caudally extends the septum principale trunci (Züllich, 1930; Francis, 1934; Boas, 1882 and present author). According to Körner (1938) and Francis (1934) the septum carotico-aorticum extends more caudally than the septum accessorium, whereas from our investigation and from Züllich (1930) it appears that the septum accessorium extends more caudally than the septum carotico-aorticum.

The terminology of the septa of the truncus arteriosus is rather divergent in the various authors. In table V the names of the septa as given by the authors are stated.

Only Körner discusses the terminology of the other writers. When considering the names of the septa we started from the presumption that the name septum aortico-pulmonale is disputable. In *Salamandra maculosa* Laur. we always find dorsally of these two septa the truncus divided into two pairs of spaces: two median root-vessels of the pulmonalis and two others: the root-vessels of the arterial arches V, also called the "third" arterial arches. We cannot agree with Greil's (1903 A) mode of expression that all these vessels are to be considered as the root-vessels of the pulmonary arches, as the arterial arches V are connected with the arterial arches IV (the systemics) and are only by the ducti Botalli connected with the arterial arches VI (the pulmonary arches). This relation we shall discuss in the following chapter. Indeed there are several Urodela – cf. Körner (1938) – where the separation in root-vessels of the arterial arches V and VI is not found at all. For those cases, however, where the separation is found the name septum aortico-pulmonale for the septum between the root-vessels of the arterial arches IV and V seems to us to be confusing. We should prefer, in agreement with Anura, the name introduced for Urodela by Züllich (1930): septum principale trunci (without including herein the caudal part of the septum medianum as Züllich does).

Körner (1938, p. 168) is of opinion that the whole of the septum medianum must be considered as a "ganz einheitliches Septum", seeing the arrangement of its musculature and because according to Greil's investigation, the septum medianum arises "als einheitliche, solide Wand."

However, although Körner (1938) does not consider the

TABLE V

	Boas (1882)	Greil (1903 A)	Züllich (1930)	Körner (1938)	Terhal
Septum between both the root-vessels of the arterial arches VI	mediane vertikale Scheidewand	septum pulmonale (mediane Scheidewand – dorsaler Abschnitt)	septum medianum interpulmonale	septum sagittale	septum medianum pulmonale
Septa (septum) between the root-vessels of the arterial arches VI and V	schräge oder vertikale Scheidewand	septum accessorium	septum pulmonale	septum intrapulmonale	septum accessorium
Septa (septum) between the root-vessels of the arterial arches V and IV	horizontale Scheidewand	septum aortico-pulmonale	septum principale trunci	septum aortico-pulmonale	septum principale trunci
Septa (septum) between the root-vessels of the arterial arches IV and III	vertikale Scheidewand	septum carotico-aorticum	septum trunci a and c	septum carotico-aorticum	septum carotico-aorticum
Septum between both the root-vessels of the arterial arches III	vertikale Scheidewand	septum caroticum (mediane Scheidewand – ventraler Abschnitt)	septum trunci b	septum sagittale	septum medianum caroticum

septum principale trunci als "einheitlich", and therefore rejects the name of septum principale trunci, this wall is, according to Greil's investigation (1903 A, p. 99), in its caudal part also to be considered as an "einheitliche(s) Septum aorticopulmonale".

Seeing the presence of the central lymph heart it seems to us hardly comprehensible how the authors can consider the septum medianum or the septum principale trunci as "einheitlich" both embryologically and seeing its musculature. Nevertheless, taking into account the position of the septa in the caudal part of the truncus arteriosus and in order to make the terminology agree with that of Rana (Gaupp, 1899), we think it best to maintain the name septum principale trunci.

From the above the name septum accessorium seems to us to be correct, while the names septum medianum pulmonale and septum medianum caroticum are given by the authors in almost the same terminology.

Züllich (1930) describes in *Salamandra maculosa* the dorsal truncus wall connected with the oesophagus by a cartilaginous mass. This relation we have not been able to discover. Probably Züllich means the cartilage of the laryngo-tracheal chamber (Francis, 1934).

Arterial arches

Own investigation

From the cranial part of the truncus arteriosus of *Salamandra maculosa* Laur. continue four pairs of arterial arches (fig. 20 and 23). Sometimes in older adult animals the arterial arches V (also called the "third" arches) may be missing on one or both sides of the truncus arteriosus (fig. 24). This relation will be discussed later on in this chapter.

Most caudally and dorsally originate the pulmonary arches (A. VI). In cranial and ventral direction arise successively the "third" arches (A. V), the systemic arches (A. IV) and the carotid arches (A. III). Even in our youngest larvae there is not the slightest indication of the arches I and II.

The bifurcation points of these successive pairs of arterial arches are lying in a plane placed caudo-dorsally to cranio-ventrally. Seen ventrally the median parts of the "third" arches (A. V) beside the truncus arteriosus partly cover those of the pulmonary arches in all the specimens, while at the same time the

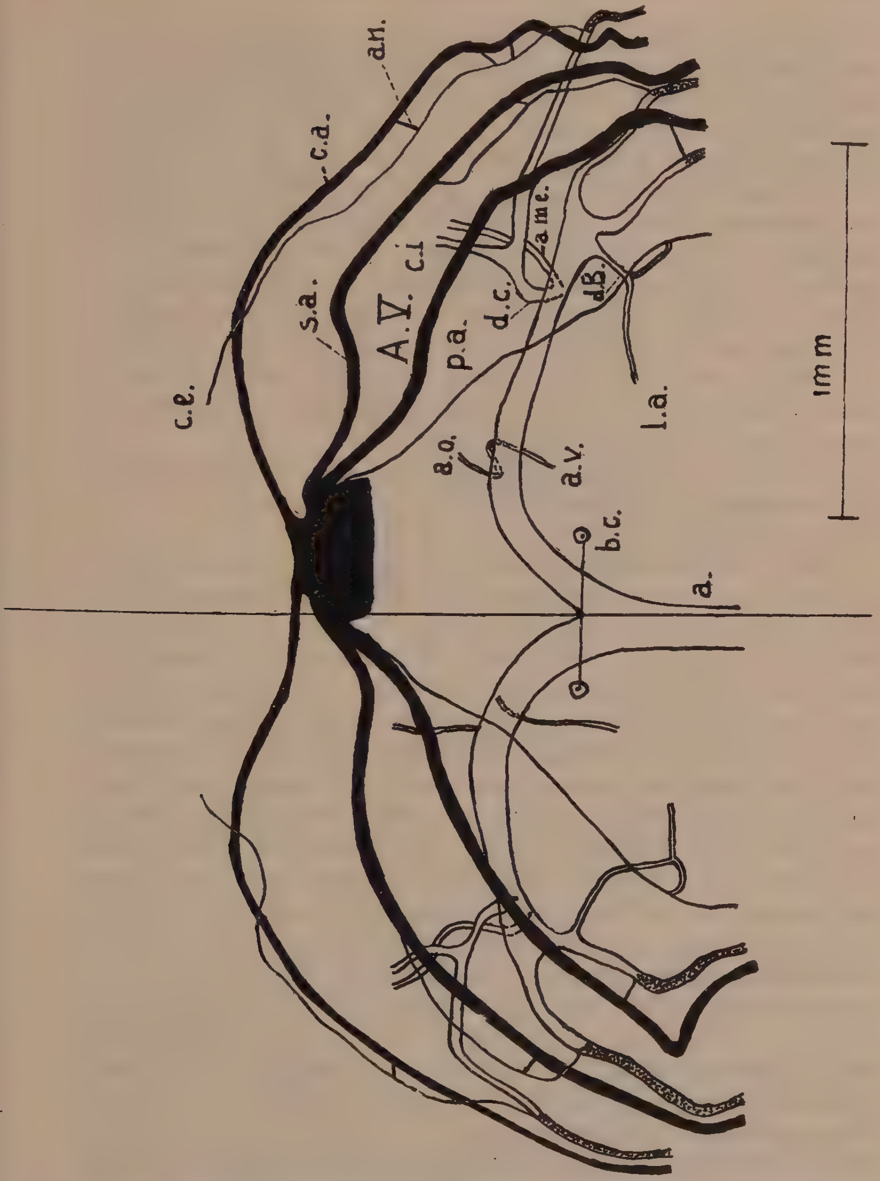

Fig. 20. Graphic reconstruction of the arterial arches of a larva of *Salamandra maculosa* Laur. (no 1) before metamorphosis.

b.c., backs of the occipital condyles; c.a., carotid arch; s.a., systemic arch; A.V., "third" arch; p.a., pulmonary arch; c.e., arteria carotis externa; c.i., arteria carotis interna; d.c., ductus caroticus; an., anastomosis; a.m.e., arteria maxillaris externa; l.a., lung artery; d.B., ductus Botalli; a., dorsal aorta; a.o. arteria occipitalis; a.v., arteria vertebralis collateralis.

like parts of the systemic arches (A. IV) partly cover those of the "third" arches (A. V), though to a less extent (fig. 20). In older larvae and adult animals the plane of the bifurcation points is directed more dorso-ventrally, so that the covering of the median parts is to a greater extent perceivable (fig. 23 and 24).

The arterial arches undergo during the development some very important changes. In order to carefully study these changes during the development graphic reconstructions were made of the arterial arches of the larval specimens, in which drawings the plane of the backs of the occipital condyles was taken as point of comparison. For want of fixed points in dorso-ventral direction the dorso-ventral obliquity of the sections could not be corrected in the drawings, so that these reconstructions are only approximately right.

In order to describe the changes of the arterial arches during the development, we shall first describe the arterial arches in the youngest larval specimen no 1 (fig. 20).

Each of the arterial arches bends from the truncus arteriosus in lateral and caudal direction towards the cartilaginous branchial arches of the visceral skeleton, in fact to the cerato-branchials. In the laterally directed parts the carotid arches are bent slightly cranially, while especially the systemic and "third" and to a less extent also the pulmonary arches possess caudally directed bends. On reaching the cartilaginous cerato-branchials they run along the ventral margins of these cerato-branchials. (These cartilaginous arches are arranged from cranially median and ventral to caudally lateral and dorsal. On the ventral margins are the gill plates hanging in ventral direction. These gill plates alter into the gills in caudal direction.)

On the boundary between the tissue round the cerato-branchials and the gill plates – thus ventrally in respect to the cartilaginous arches – are the bloodvessels mentioned above (fig. 21). Each of the arterial arches runs caudo-laterally into the gill plates and gills. The bloodvessels within the gill plates and within the gills have not been further examined by us. Among the arterial arches the pulmonary arches are very narrow (10 micra), whereas the carotid arches are wider (40–50 micra); the systemic arches and the "third" arches having the largest diameter and agreeing with each other (60–70 micra).

The gill veins coming from the gills are situated ventrally of the commissurae terminales of the cerato-branchials, and bend medianwards at the caudal and median ends of the cerato-branchials. Caudally of the commissurae terminales there arises from each of the gill veins III a thinner branch running in ventral and cranial direction. This branch, the origin of the arteria carotis externa, is situated along the median side of the cerato-branchial (fig. 21). This bloodvessel follows the cerato-branchial entirely, to extend at the headward end of it in cranial direction. Between this arteria carotis externa and the carotid arch we find some small anastomoses lying on the median side of the cerato-branchial, three on the left and one on the right side of the animal.

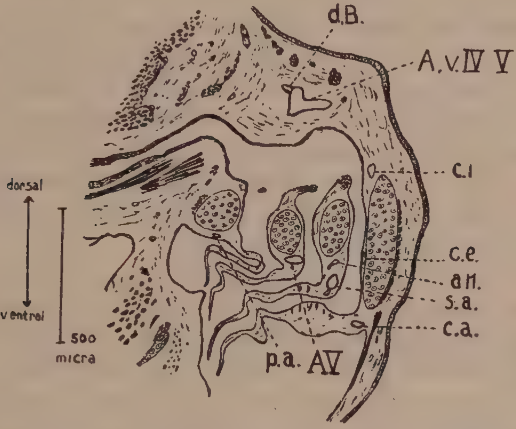

Fig. 21. Transverse section through the region of the cerato-branchials in a larva of *Salamandra maculosa* Laur. before metamorphosis (no 1). c.a., carotid arch; s.a., systemic arch; A.V. "third" arch; p.a., pulmonary arch; an., anastomosis; c.e., arteria carotis externa; c.i., arteria carotis interna; d.B., ductus Botalli; A.v.IV-V., junction of the gill veins IV and V.

Gill vein IV bends in the same way from the gill medianwards. Here, too, there arises caudally of the commissurae terminales a long thin branch in cranial and ventral direction, extending cranially on the ventral side of the cerato-branchial II (fig. 21). This bloodvessel is lying between the cerato-branchial and the systemic arch, into which it opens in cranial direction. In the space between the bloodvessel just described and the systemic arch there is a thin anastomosis on either side of the animal.

Gill vein V bends medianwards at the cranial end of the cerato-branchial III. Caudally of the commissurae terminales this vein, too, gives rise to a very short branch, which immediately grows together with the "third" arch. Between this small bloodvessel and the "third" arch no anastomosis is to be found.

In our opinion there cannot be any question of a gill vein VI. Behind the caudal end of the cerato-branchial IV is a bloodvessel – a branch of the pulmonary arch – which is connected with the lung artery. This lung artery runs in lateral and caudal direction to the lung; in cranial direction it extends as ductus Botalli, and is as such connected with the root-vessel of the dorsal aorta. Whereas the pulmonary arch is very thin (10 micra), the lung artery and the ductus Botalli are much wider (30 micra). The connection between the pulmonary arch, and the lung artery is of a small diameter (10 micra).

The gill veins IV and V described above, as well as the ductus Botalli, are connected with one another in cranial direction. On the left side these three bloodvessels unite in the same place, on the right side the ductus Botalli first unites with gill vein V and these two unite with gill vein IV. In this way originate the dorsal aorta roots. These aorta roots bend medianwards to meet each other and form the dorsal aorta.

Gill vein III runs parallel with the aorta root and extends cranially of the connection of gill vein IV with gill vein V headwards. It is the origin of the arteria carotis interna. By means of a bloodvessel, the ductus caroticus, this arteria carotis interna is connected with the aorta root.

Just beside the connection of the ductus caroticus with the aorta root, and even connected with the ductus caroticus, arises a small bloodvessel directed cranially, the origin of the arteria maxillaris externa.

In the neighbourhood of the median plane arises at the cranial part of the aorta root the arteria vertebralis collateralis. This bloodvessel bends dorsally across the aorta root to run in caudal direction. Connected with the arteria vertebralis (on the left side) or arising separately on the aorta root (on the right side) we find the origin of the arteria occipitalis running in cranial direction.

In our study of the changes of these bloodvessels during metamorphosis we first tried to obtain an impression of the caudal movement which the arterial arches experience.

TABLE VI

Number of animal	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Distance between the caudal planes of the cond. occipitales and the junction of the aorta roots [1])	10	20	120	150	160	330	390	340	360	320	320	390	280	440	280	210	190
Distance between the caudal planes of the cond. occipitales and the most cranial point of the dorsal aorta root	270	390	390	470	425	350	280	380	510	455	380	535	760	460	470	810	820
Distance between the front of the bifurcation of the truncus arteriosus and the caudal planes of the cond. occipitales	750	750	910	900	870	910	260	520	190	410	470	360	610	200	220	670	750
Average distance between the backs of the foramina nervi spinalis of the vertebrae II, III, IV and V	380	430	460	590	640	700	690	690	760	660	690	790	710	610	620	600	570

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[1] all distances in micra

As was also stated above, the heart and also the truncus arteriosus move early already during metamorphosis in caudal direction. In order to ascertain whether and how far the arterial arches also experience this caudal movement we measured in the successive specimens – in the same way as described in the chapter dealing with the position of the heart – the distances between the occipital condyles and the point of the junction of the aorta roots lying caudally of the condyles, together with the distances between the caudal planes of the occipital condyles and the most cranial point of the dorsal aorta root lying cranially of the occipital condyles. These last figures were obtained by taking the average of the distances measured on the left and on the right in each animal.

The distances measured are to a very small extent subject to a mistake owing to the dorsal-ventral obliqueness of the sections, as the aorta roots are situated only slightly ventrally of the occipital condyles.

In table VI these distances are given together with the figures concerning the distances between the front of the truncus arteriosus and the backs of the occipital condyles, as given in table IV. In this table VI are also once more given the figures of the average distances between the backs of the foramina nervi spinalis of the second, third, fourth and fifth vertebrae. In fig. 22 these figures are graphically represented.

From a comparison of these distances it appears that the junction of the aorta roots also moves in a caudal direction. This might partly be ascribed to growth, but it is as certain that this movement takes place by an absolute movement in a caudal direction, as the distances between the junction of the aorta roots and the occipital condyles get proportionally larger than only the skeleton growth could make us suppose.

This movement appears to occur to a very great extent in the younger specimens (nos 1 to 6). However, it occurs to a much smaller extent than the caudal movement of the cranial point of the truncus, so that a hypothetical transverse plane containing the front of the truncus and the junction of the aorta roots, which plane, in the youngest specimens, is placed from cranio-ventrally to caudo-dorsally, is gradually placed more dorso-ventral (fig. 23). In the adult animals this plane slants just in the other direction from caudo-ventrally to cranio-dorsally, the front of the truncus being found further back from

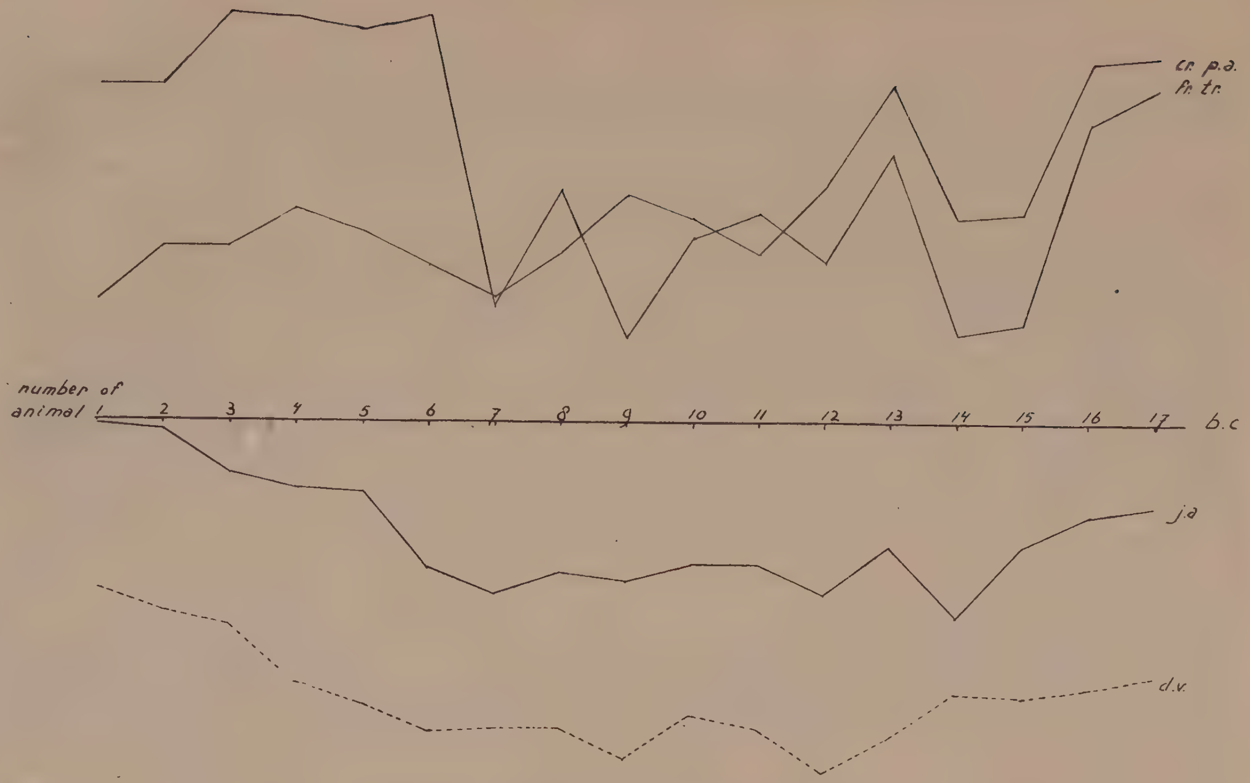

Fig. 22. Graphical representation of the position of the arterial arches and the truncus arteriosus of *Salamandra maculosa* Laur. in relation to the occipital condyles.

b.c., backs of the occipital condyles; j.a., position of the junction of the aorta roots; cr.p.a., position of the most cranial point of the dorsal aorta root; fr.tr., position of the front of the truncus arteriosus. Distances between d.v. and b.c. showing the length of vertebrae in the successive specimens.

the occipital condyles than the junction of the aorta roots (fig. 24).

Difficult to represent in measures are the movements experienced by the arches between these two points. With the revolving of the above plane the arterial arches lying more or less in it must generally follow this movement. From a study of the graphic reconstructions as compared with the situation of the occipital condyles it appears that these arterial arches, too, experience not only a relative caudal movement owing to the growth of the animal, but also an absolute caudal movement. This holds good especially in the case of the ventral arterial arches, in connection with the greater caudal movement of the truncus arteriosus. In this movement the ventral arterial arches at the same time draw closer to each other in caudal-cranial direction and the direction of these ventral parts of the arches becomes more transversal instead of median-cranial to lateral-caudal, as the lateral parts of the original arches move comparatively less caudally (fig. 20, 23 and 24). This movement is connected with the reduction of the cerato-branchials. In the case of the dorsal parts of the arterial arches the caudal movement of the aorta roots is more concerned with their junction than with the arches themselves. As appears from table VI the cranial points of the dorsal aorta roots undergo no – or, in the beginning of the metamorphosis only a small – caudal movement. In the older specimens these aorta roots take up a more cranial position again, partly perhaps because after a caudal movement they come to be situated more headwards by the growth of the animal, partly perhaps because the whole of the bloodvessel system has not experienced a caudal movement to such an extent as is the case with other animals (specimens nos 13, 16 and 17). All the same in these three cases the above points are situated more cranially than the front of the truncus arteriosus, contrary to the younger larvae (fig. 22).

The total length of the arches seems to us to increase less than the bodily growth during the development, so that a relative shortening of the arches takes place. While this holds good for the ventral parts of the arches, the dorsal parts seem to show no relative shortening, but a growth in proportion to the skeleton growth or even exceeding it (fig. 20, 23 and 24). All these changes are difficult to measure, owing to the bends of the arches both in cranial and caudal, but especially in dorsal and ventral directions.

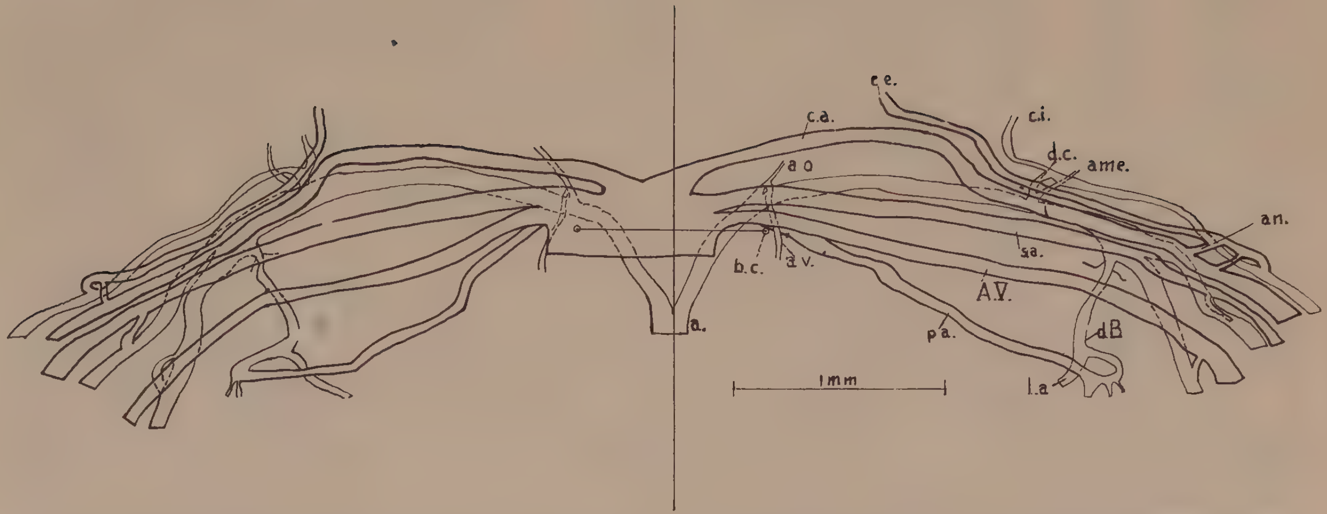

Fig. 23. Graphic reconstruction of the arterial arches of a larva of *Salamandra maculosa* Laur. (no 7) during metamorphosis. b.c., backs of the occipital condyles; c.a., carotid arch; s.a., systemic arch; A.V., "third" arch; p.a., pulmonary arch; c.e., arteria carotis externa; c.i., arteria carotis interna; d.c., ductus caroticus; an., anastomosis; a.m.e., arteria maxillaris externa; l.a., lung artery; d.B., ductus Botalli; a., dorsal aorta; a.o., arteria occipitalis; a.v., arteria vertebralis collateralis.

Simultaneously with the changes in the situation of the bloodvessels as described above, a change is perceived in the relations of diameter of the lumen of the bloodvessels under discussion, while together with the disappearance of gills and gill plates the bloodvessels belonging to them disappear.

The changes in the relative width of the various bloodvessels are to be ascribed to the quicker or less quick increase in diameter during the growth.

The increase in relative thickness holds especially good in the case of the long anastomoses between the systemic arch and the gill vein IV, and the short anastomoses between the "third" arterial arch and the gill vein V. As in older specimens these two anastomoses possess the same thickness as the arches belonging to them, they make one continuative whole of the dorsal and ventral parts of the arches (fig. 20, 23 and 24). Whereas in our youngest specimens the systemic arches and the "third" arches are thickest, and thicker than the carotid arches, which, in their turn, are thicker than the pulmonary arches, it appears that during the development, before metamorphosis already (specimen no 5), the systemic arch prevails in diameter. At the same time the pulmonary arch increases in diameter in relation to the "third" arch and will even surpass it in older larvae and adult animals, and will reach the same width as the carotid arch or even surpass it (fig. 20, 23 and 24).

In all the young animals examined by us the "third" arch is present on either side. In the adult animals, on the contrary, we found only in two specimens the "third" arch bilaterally present (nos 18 and 20). In specimen no 19 the "third" arch is only present on the left, and in no 21 only on the right side. In specimen no 22 the arch is missing on both sides, except for a small tube, ending blind, on the left side of the truncus arteriosus. As in the seventeen youngest specimens examined by us the "third" arches are present and are missing rather frequently in the older animals this disappearance must take place considerably after the end of the metamorphosis. Save the small tube in specimen no 22 no rests of the "third" arches are to be found in the adult animals. In all the cases where the "third" arch is missing the cavity of the root-vessel of the "third" arch is present in the truncus arteriosus, it ends, however, blind.

The lateral part of the carotid arch in connection with the basal part of the arteria carotis externa arising on gill vein III

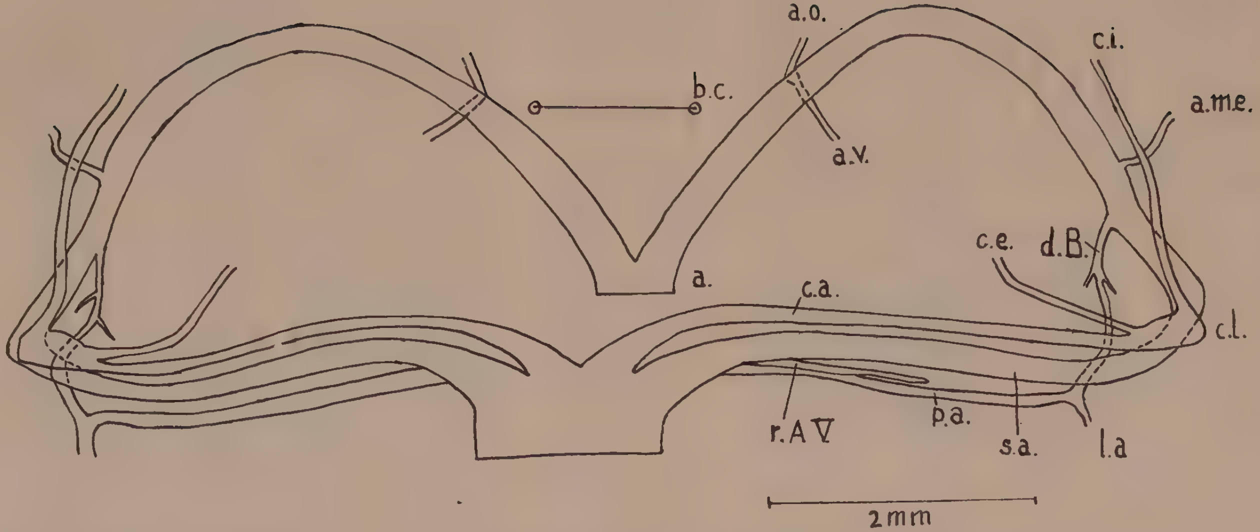

Fig. 24. Graphic reconstruction of the arterial arches of an adult *Salamandra maculosa* Laur. (no 22). b.c., backs of the occipital condyles; c.a., carotid arch; s.a., systemic arch; r.A.V., remainder of the "third" arch; p.a., pulmonary arch; c.e., arteria carotis externa; c.i., arteria carotis interna; a.m.e., arteria maxillaris externa; l.a., lung artery; d.B., ductus Botalli; a., dorsal aorta; a.o., arteria occipitalis; a.v. arteria vertebralis collateralis; c.l., carotid labyrinth.

gives in the specimens after metamorphosis rise to the formation of the carotid labyrinth (carotid gland). Especially owing to this development the carotid arch undergoes a more relative shortening than the other arches. This development will be discussed separately in this paper.

The part of the gill vein III, which later becomes the basal part of the arteria carotis interna follows in general the movement of the aorta root, while the basal part of the arteria carotis externa arising on gill vein III follows the caudal movement of the carotid arch, so that in adult animals, too, the basal part of the arteria carotis externa remains lying partly parallel to the carotid arch, and the basal part of the arteria carotis interna to the aorta root.

While in all the young animals the arteria carotis interna remains connected with the aorta root by means of the ductus caroticus, neither this duct nor any rest of it is to be found in the adult animals, so that this connection disappears long after metamorphosis.

The arteria maxillaris externa is in all the young specimens connected with the ductus caroticus, or can by means of a communal opening with the ductus caroticus open into the aorta root. However, as the ductus caroticus has disappeared in the adult animals the arteria maxillaris externa is here connected direct with the aorta root.

Whereas the pulmonary arch grows thicker and obtains the same width as the lung artery, the diameter of the ductus Botalli decreases (fig. 23 and 24). In not one case is the ductus Botalli missing. Into the ductus Botalli open one or two smaller blood vessels. The ductus Botalli opens into the aorta root in about the same place as the "third" arch, although in a number of specimens the ductus Botalli opens first into the "third" arch and a little more cranially the latter opens into the aorta root. In a few specimens the ductus Botalli opens quite separately into the aorta root. A remarkable situation was found in specimen no 5, because here on both sides of the animal we found two ductus Botalli present, one of them opens into the aorta root, the other into the "third" arch.

The arteria vertebralis collateralis and the arteria occipitalis cannot only separately, but in most cases by means of a communal opening, open into the aorta root.

On both sides of the truncus arteriosus in *Ambystoma mexicanum* Shaw we invariably find four arterial arches.

However, the situation was often such that the pulmonary arch arises from the inside of the proximal part of the "third" arch – exactly there where this leaves the truncus arteriosus (fig. 25). This is not only the case in one of the young larvae (no 26) but also in older animals (nos 31, 32 and 33) and in one transformed animal (no 38). So in these cases there are only six root-vessels in the cranial part of the truncus arteriosus.

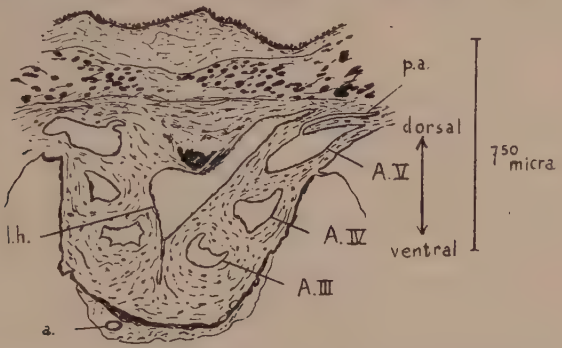

Fig. 25. Transverse section through the truncus arteriosus of a larva of *Ambystoma mexicanum* Shaw (no 26).
p.a., pulmonary arch; A.III, A.IV and A.V, root-vessels of the arterial arches l.h., central lymph heart; a., artery.

In young larvae the bloodvessel complex is generally arranged and composed in the same way as in the young larvae of *Salamandra maculosa* Laur.

The pulmonary arches are very thin. The "third" arches are here already less wide than the systemic arches. Between the carotid arch and the arteria carotis externa we find numerous anastomoses.

Gill vein V and the ductus Botalli unite and only much more cranially there follows the junction with gill vein IV, a situation found in all the other animals (fig. 26) and which is characteristic in relation to the situation in *Salamandra maculosa* Laur.

Already in these young larvae the ductus Botalli is a gradual connection of the lung artery with the gill vein V, into which a thinner connection with the pulmonary arch opens.

The arteria carotis interna is in the youngest specimens

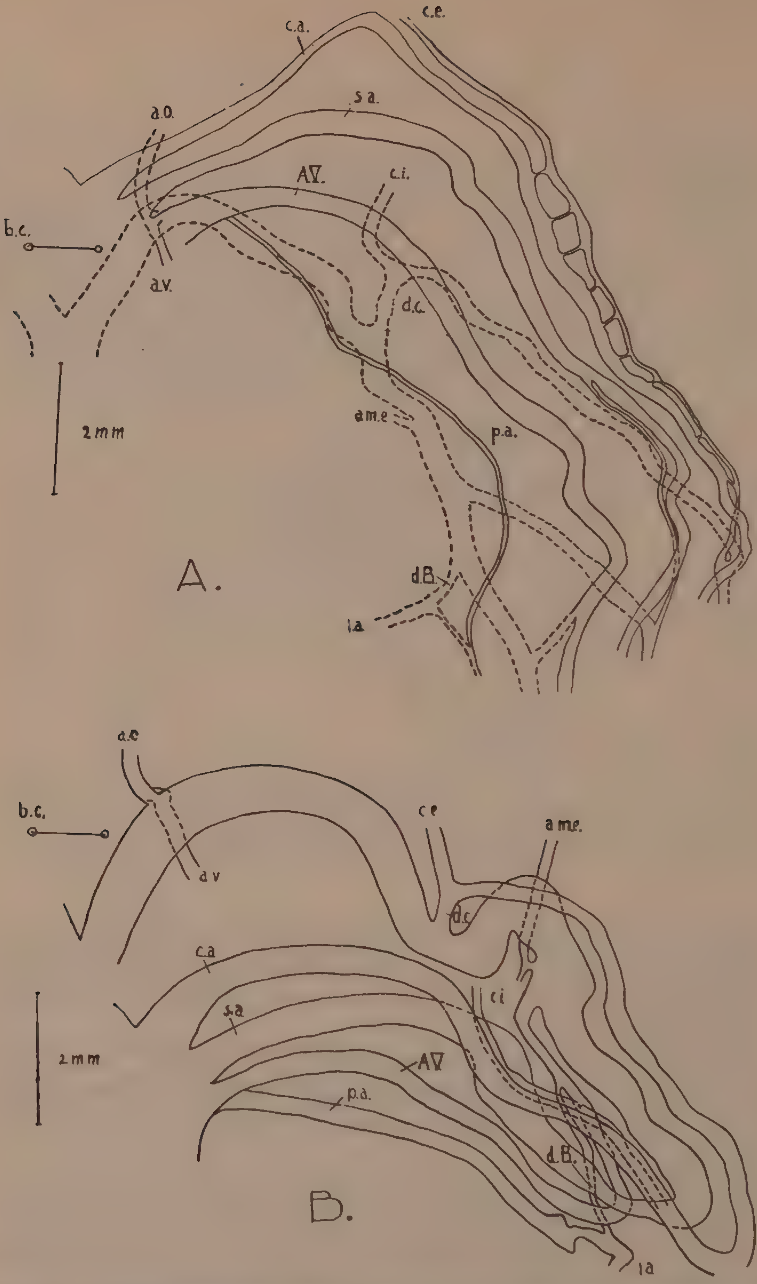

Fig. 26. Graphic reconstructions of the arterial arches of *Ambystoma mexicanum* Shaw.

A. Neotonic animal (no 28).

B. Transformed animal (no 35).

b.c., backs of the occipital condyles; c.a., carotid arch; s.a., systemic arch; A.V., "third" arch; p.a., pulmonary arch; l.a., lung artery; c.e., arteria carotis externa; a.m.e., arteria maxillaris externa; c.i., arteria carotis interna; d.B., ductus Botalli; d.c., ductus caroticus; a.v., arteria vertebralis collateralis; a.o., arteria occipitalis.

examined by us connected with the aorta root by a very long ductus caroticus. The arteria maxillaris externa is first perceivable as growing in specimen no 24. In older animals this vessel is much more clearly visible. In all the animals it opens out laterally of the opening of the ductus caroticus into the aorta root (fig. 26). Only specimen no 25 forms an exception, as in the left part of the animal the arteria maxillaris externa arises on the vessel from gill vein V to the aorta root.

The arteria vertebralis collateralis and the arteria occipitalis open out together into the aorta root in all larvae and adult animals (fig. 26).

Whereas in the young larvae the truncus arteriosus and ventral arterial arches are situated far cranially of the occipital condyles, the truncus arteriosus and ventral arterial arches have moved more caudally in the older neotenic animals. The truncus arteriosus lies in these animals in the same sections with the occipital condyles (fig. 26, A). The dorsal parts of the arterial arches on the other hand have remained in the same position as compared with the younger larvae. In these neotenic animals the composition of the bloodvessel system is fairly equal to that in young larvae. The pulmonary arches are here still very narrow. The lung artery is, here too, a gradual extension of the ductus Botalli into which the very thin branch of the pulmonary arch opens.

Between the connection of the ductus Botalli and gill vein V and the junction of the latter with gill vein IV remain large distances. The ductus caroticus is much shorter (fig. 26) in these specimens than is the case in the younger larvae.

During metamorphosis a further caudal movement of the ventral bloodvessel complex takes place, so that in the transformed animals this lies caudally of the occipital condyles and also caudally of the junction of the aorta roots.

In the animals during metamorphosis the aorta roots show bends probably because a slight caudal movement of these roots also takes place.

In the transformed animals each of the arches forms one continuous whole, the lateral parts of which lie far caudally in respect to *Salamandra maculosa* Laur. The bends in the aorta roots are here also present.

The pulmonary arch has increased in diameter.

In relation to the neotenic animals the ductus Botalli is narrow so that the lung artery here appears more as an extension of the pulmonary arch. The "third" arch is clearly thinner than the systemic arch; in no 34 even very thin.

Discussion

After the older publication by Rusconi (1854) it was only Boas (1882) who wrote about the arterial arches of the *Salamandra* larva.

Changes of these arterial arches in urodelan larvae are also described by Boas (1882) for *Salamandra*, while as far as we know these changes have of late been described only by McMullen (1938) for *Desmognathus fuscus*, *Plethodon cinereus*, *Eurycea bislineata* and *Gyrinophilys porphyriticus*.

These two authors do not, however, describe any changes in the position of the bloodvessels.

Only very little can be added to the excellent description by Boas (1882) about four successive larval stages of *Salamandra*.

Between the systemic arch and its corresponding vein Boas usually finds more anastomoses, whereas we could only discover one. The arteria maxillaris externa (Bethge, 1898) (arteria mandibulo-jugularis, Drüner, 1904) (arteria pharyngea ascendens, Osawa, 1902; Francis, 1934), but also the arteria vertebralis collateralis and the arteria occipitalis (Bethge, 1898) (the palato-nasal artery, Francis, 1934), which were found by us in our specimen no 1 already, are not described by Boas although, seeing the text of his Fig. 37, this last vessel was known to him.

McMullen (1938), too, states that no arteria maxillaris externa is present in the animals examined by him before metamorphosis; according to him these arteries develop during metamorphosis. This opinion cannot be correct as far as *Salamandra maculosa* Laur. and *Ambystoma mexicanum* Shaw are concerned.

About the arterial arches of adult *Salamandra maculosa* we find besides in older authors, Rusconi (1854) and Fritsch (1869), also important data in Boas (1882 and 1888), Bethge (1898), Königstein (1903) and Francis (1934).

In *Salamandra maculosa* most authors usually find four pairs of arterial arches, seldom three. It is a pity that most of these authors do not give the number of animals examined, nor the number of cases in which they found three or four pairs of arterial arches. Seeing the data in literature and our own finds, we are of opinion that in *Salamandra maculosa* Laur. the number of arches is exceedingly variable, so that in most cases four pairs of arches are to be found, though three pairs also occur rather much, while in this case either on the left side or on the right the "third" arch may be present.

In *Ambystoma mexicanum* Shaw we always find four pairs of arterial arches, also in the transformed specimens.

Michon (1937), too, invariably found four pairs of arterial arches in *Triton marmoratus* Latr. Therefore, we cannot agree with Körner's (1938, p. 169) remark: "dass vier Arterienbogen bei den Schwanzlurchen nur verhältnismässig selten vorkommen und auch innerhalb einer Art nicht das regelmässige Verhalten darstellen."

If in *Salamandra maculosa* Laur. this "third" arch is present, it usually opens out into the systemic arch in the same place as the ductus Botalli, or the "third" arch and the ductus Botalli first join and then open out together into the systemic arch.

The situation as described by Francis (1934) for *Salamandra salamandra* L. that the ductus Botalli opens out into the systemic arch cranially from the opening of the "third" arch into the systemic arch, seems to us rather exceptional.

Boas (1882, p. 539) thought *Siredon* to be a "Stufe" between the *Salamandra* larva and *Siren*, especially from the fact that the junction of the ductus Botalli in *Siredon* with gill vein V on the one hand, and the junction of gill vein V with gill vein IV on the other hand lie farther apart than is the case in *Salamandra*.

It may be interesting to point out here that the cases mentioned by us, in which the pulmonary arch originates from the proximal part of the "third" arch, also suggest the relation in *Siren* as described by Boas (1882), where the pulmonary arch originates from the "third" arch, be it more laterally of the bifurcation of the "third" arch from the truncus arteriosus.

Only in a few cases (Boas, 1882; Francis, 1934, once on one side) in *Salamandra* the ductus caroticus is found. In the adult animals of *Salamandra maculosa* Laur. examined by us this connection between the arteria carotis interna and the aorta root is always absent.

Although the arteria vertebralis collateralis usually arises together with the arteria occipitalis as Bethge (1898) described, it cannot be denied that in *Salamandra maculosa* Laur. they sometimes arise separately from the aorta root, as is also stated by Francis (1934).

Bethge (1898) and Francis (1934) describe in *Salamandra* a branch of the systemic arch (the cutaneus branch; Francis). In the animals examined by us this bloodvessel was only found in one specimen of *Salamandra maculosa* Laur.

V. THE PERICARDIUM

Own investigation

The heart of *Salamandra maculosa* Laur. is surrounded by the pericardial cavity which is bounded by a fibrous membrane, the pericardium (fig. 17).

The caudal point of the pericardial cavity lies ventrally right of the cranial liver-top. The vena cava posterior penetrates from ventrally left into the caudal part of the pericardial cavity and lies against and is connected with the left pericardial wall. Slightly cranially from the caudal pericardium top the caudal part of the pericardial cavity is divided into a smaller dorsal and a larger ventral room by a frontally placed membrane (Gubernaculum cordis, Fritsch, 1869; Membrana hepato-pericardiaca, Mathes, 1895; mesocardial ligament, Francis, 1934).

The vena cava posterior continues cranially from the left pericardial wall on this frontal membrane, gradually changing into the sinus venosus.

The above mentioned dorsal pericardial room in the most caudal part of the pericardial cavity is divided into a narrow left part and a wider right one by a median wall. These two cavities, ending blind in caudal direction, are the remainders of the ductus pleuro-pericardiaci (recessus pleuro-pericardiaci). The pericardial cavity is already in the youngest specimens examined by us wholly separated from the pleuro-peritoneal cavity. The median wall between the two cavities, the continuation of the ligamentum hepato-entericum, is in cranial direction not very high. On its cranial edge lies the vena pulmonalis, running from the dorsal pericardial wall to the sinus venosus.

Against the right part of the frontal mesocardial ligament lies the ventricle, in such a way, however, that the most caudal ventricle top remains free.

The mesocardial ligament continues cranially to the caudal edges of the two ducts of Cuvier. Caudally from this line the sinus venosus and the ventricle are closely connected with the mesocardial ligament.

The parts of the heart lying more cranially are not attached to the pericardium. On the other hand in the cranial part of the pericardial cavity we find the dorsal wall of the truncus arteriosus, slightly caudally from the bifurcation of the pulmonary arches, lying against the dorsal pericardial wall again.

Thus between the dorsal pericardium wall and the dorsal truncus wall a conical cavity is formed, ending blind cranially.

When studying the proportions of the heart and the pericardial cavity, it appears that in our youngest specimens (nos 1–4) the pericardial cavity is relatively wide, and that only in the older specimens the heart completely fills the cavity. However, the width of the pericardial cavity in younger larvae is not such as to enable the heart to move within the cavity in its caudal movement. From a comparison of the situation of the heart apex and the caudal pericardial top it appears that both the heart and the whole pericardium move in a caudal direction. To this it is attributable that in older specimens the cranial liver-top lies proportionally more cranially in respect to the caudal pericardium point than in younger specimens.

The cranial attachment of the dorsal wall of the truncus arteriosus to the pericardial wall remains the same, i.e., slightly caudally from the bifurcation of the pulmonary arches. The conical cavity, however, between the dorsal wall of the truncus arteriosus and the pericardium disappears.

The continuation of the ligamentum hepato-entericum is also present in the adult animals, although it does not always extend wholly from the caudal pericardial wall to the lung vein.

In young larval specimens of *Ambystoma mexicanum* Shaw the pericardium is here, too, very wide. The continuation of the ligamentum hepato-entericum is in the young larvae already very low, in accordance with the fact that the vena pulmonalis reaches the sinus venosus far caudally.

In the neotenic and transformed animals the pericardium cavity is almost wholly filled by the heart.

Discussion

The development of the pericardium in Urodela (*Salamandra* *maculata* and *Salamandra atra*) is discussed by MATHES (1895). FRITSCH (1869) gives some vague descriptions about the pericardium of adult Urodela. FRANCIS (1934) describes the pericardium of the adult *Salamandra salamandra* L., but does not seem to have perceived the continuation of the ligamentum hepato-entericum in the pericardial cavity.

VI. THE CENTRAL LYMPH HEART

Own investigation

In the youngest larvae of *Salamandra maculosa* Laur. already we find between the root-vessels of the arterial arches the caudal basis of a central lymph heart in the truncus arteriosus (fig. 17).

This basis is directed caudally with a conical top, and develops cranially into a central space. The root-vessels of the arterial arches surround the basis of the lymph heart ventrally and laterally. Dorsally the basis is covered by the connective tissue of the truncus wall, outside of which the cross-striped muscular layer of the truncus is situated. The central space of the lymph heart lies dorsally of the arterial arches where they leave the pericardial cavity successively, and is dorsally covered by the extension of the cross-striped dorsal truncus musculature lying outside the pericardial cavity. Outside the pericardium this extension of the dorsal truncus-musculature continues dorsally of the central cavity of the lymph heart as a cross-striped longitudinal muscular band. Cranially of the carotid bifurcation this muscular band joins the ventral musculature of the truncus arteriosus. This junction is not yet complete in the youngest larvae, but is so in the older specimens.

The central lymph heart ends cranially into two blindly ending tops, which are separated from each other by the above mentioned junction of the dorsal and ventral musculature of the truncus arteriosus.

Two lymph vessels open on either side into the central space. In these openings valves are found.

In older larvae (fig. 18) the caudal basis can be followed up more caudally into the truncus arteriosus than in younger ones, which might be explained by the supposition that the root-vessels in older larvae are connected with each other over a larger distance to the expense of the size of the central cavity.

The cranially directed tops are in older larvae shorter as compared with those of the younger larvae.

The central lymph heart in *Ambystoma mexicanum* Shaw corresponds with the situation described for *Salamandra maculosa* Laur. (fig. 25).

Its blindly ending cranial tops are not distinguishable.

Discussion

Although Beddard (1903) observed a cavity between the root-vessels of the arterial arches in the truncus arteriosus of *Megalobatrachus japonicus*, Greil (1903 A) was the first to recognize and describe in the heart of *Salamandra atra* this cavity as a central lymph heart.

Also in Hoyer and Udziela (1912) we find data on the lymph heart of the larvae of *Salamandra maculosa* Laur. These two authors describe the muscular band on the dorsal wall of the cranial part of the lymph heart as consisting of smooth muscular fibres. In older larvae and adult animals, however, we invariably found cross-striped fibres in accordance with the fact that this band is an extension of the cross-striped musculature of the truncus arteriosus.

Francis (1934) gives a detailed description of the situation in adult *Salamandra salamandra* L.

Körner (1938) finds the lymph heart in all the Urodela examined by him, except in *Proteus anguineus*.

For the remark by Benninghoff (1933) as quoted in this paper in the part dealing with the truncus arteriosus, about the musculature of the truncus wall to our opinion no proof is given in literature.

VII. THE BLOODVESSELS OF THE HEART

Own investigation

As early as in the youngest larval specimens of *Salamandra maculosa* Laur. examinated we find a bloodvessel on the dorsal wall of the truncus arteriosus, running lengthways across it, which vessel is, especially in the adult animals, clearly perceivable. The construction of the wall of this vessel proves that it is an artery. For its whole length this artery is exactly median in position, it runs dorsally of the cross-striped musculature of the truncus arteriosus.

In the older larvae, but especially in the adult animals (fig. 19), we find a few small branches of this artery penetrating into this musculature. In caudal direction it may be followed up to the change of the truncus arteriosus into the bulbus cordis. In the bulbus wall we do find some smaller bloodvessels connected with the above mentioned vessel, but these do not show any regular arrangement.

The artery continues in cranial direction outside the pericardium, where it is situated in the connective tissue between the M.M. recti cervici. Although outside the pericardium it is difficult to perceive in our sections, we think it possible in some cases to prove a communication of this artery with both rami musculares for these muscles, branches of the right and the left arteria carotis externa.

Also in older larvae a clear heart vein can be found. In very young larvae the right duct of Cuvier lies against and is closely connected with the dorsal cranial wall of the ventricle. In the older larvae, however, the right duct of Cuvier is more separated from the ventricle, but remains connected with the dorsal and dorsal left parts of the cranial ventricle wall by means of a flat bloodvessel opening into the duct of Cuvier. This vessel penetrates deeply into the furrow between the atrium and the ventricle.

The penetration of ramifications of this bloodvessel into the musculature of the ventricle is difficult to perceive in larvae. In adult animals, however, we think it possible to prove this penetration.

In older larvae and adult animals we find, in the epicardium of the bulbus cordis, a network of smaller vessels communicating with the capillaries of the musculature of the bulbus cordis. Such vessels are also present in the epicardium of the cranial ventricle wall. In the epicardium of the bulbus cordis these vessels unite into two larger ones on the left ventral and the right dorsal wall of the bulbus cordis. Blood-corpuscles are not found in these vessels, so that a doubt arises whether these spaces are indeed to be considered as bloodvessels. In the adult animals, on the other hand, we think it possible to perceive a communication of this epicardial vessel network with the above mentioned heart vein.

A similar artery on the dorsal wall of the truncus arteriosus as described for *Salamandra maculosa* Laur. is also found in *Ambystoma mexicanum* Shaw.

The ramifications of this vessel over the walls of the truncus arteriosus and the bulbus cordis are very clear. In no 26 a vessel ramifying across the truncus and bulbus walls and extending cranially in the same way as the above mentioned dorsal artery is situated on the ventral wall of the truncus arteriosus (fig. 25).

The heart vein in *Ambystoma mexicanum* Shaw is not clearly separated from the right duct of Cuvier. The epicard vessels of the ventricle and bulbus cordis walls are closely connected with the right duct of Cuvier by means of narrow capillaries.

Discussion

About bloodvessels in the heart of Urodela we find many data, which do not always agree, in the literature consulted.

Hyrtl (1858 and 1864) describes for numerous Urodela (*Proteus*, *Siren*, *Menobranchus*, *Menopoma*, *Triton*, *Pleurodeles*, *Salamandra* and *Pseudotriton*) an arteria cardiaca (arteria coronaria or arteria bulbi) arising from the right arteria carotico-lingualis, only providing the walls of the bulbus arteriosus with blood vessels. One case of *Salamandra* only is figured by Hyrtl (1864), i.e. a drawing of the heart of *Salamandra maculosa* in which, however, the vessel is shown on the ventral truncus wall.

A heart artery upon the dorsal surface of the truncus arteriosus is found in Königstein (1903) for *Menopoma giganteum* and in Beddard (1903) for *Megalobatrachus japonicus*.

According to Beddard this artery should only extend up to the ventricle; according to Königstein it should ramify across the dorsal and ventral ventricle walls.

According to Königstein this bloodvessel arises from the truncus arteriosus; according to Beddard it communicates with the "third" arch.

From the presence of a heart vein Hyrtl (1864 and 1865) draws the conclusion that there is also an artery present in the heart of *Cryptobranchus japonicus*, although he could not find this artery.

In *Salamandra maculata*, too, Königstein (1903, p. 313–314) finds an artery, a branch of the arteria carotis externa, which "sich an den Aortenbogen und am Bulbus verteilt, das Herz selbst jedoch nicht erreicht".

The ramification of this vessel over the arterial arches could not be discovered by us. Yet we are of opinion that the artery described by HYRTL and the one meant by KÖNIGSTEIN in *Salamandra* are homologous with the artery described by us. This artery is evidently not homologous with the above mentioned artery described by KÖNIGSTEIN and BEDDARD for *Menopoma giganteum* and *Megalobatrachus japonicus*, for with regard to this latter vessel for *Menopoma giganteum* KÖNIGSTEIN (1903, p. 317) says: "Ausser der Coronar-Arterie besteht noch ein eigener nur für die Ernährung der Aortenbogen und den Bulbus bestimmter Ast der Carotis, der schon bei *Salamandra* Erwähnung fand".

KÖRNER (1938, p. 172) always found vessels in the animals examined by him "die von aussen an den Truncus arteriosus und den Bulbus cordis herantreten und Äste in die Wand hineinschicken". For two specimens of *Ambystoma mexicanum* he describes a number of vessels to the right on the surface of the ventricle in an epicardial thickening, from which ramifications penetrate into the musculature of the ventricle. In *Molge viridescens* and *Euproctus asper* KÖRNER found vessels penetrating into the bulbus wall from the bulbus lumen.

HYRTL (1864 and 1865) gives for *Salamandra*, *Proteus*, *Triton* and *Cryptobranchus japonicus*, KÖRNER (1938) for *Pleurodeles waltlii*, the presence of a heart vein in about the same place as described by us for *Salamandra maculosa* Laur.

REESE (1906) only gives vague hints about vessels on the wall of the heart of *Cryptobranchus alleghaniensis*, which bloodvessels shown on the ventricle wall of his figure are evidently also ramifications of the above mentioned heart vein.

FRANCIS (1934, p. 191), too, describes the heart vein for *Salamandra salamandra* L., which "from the ventricle enters the right ductus Cuvieri on its ventral aspect at the right margin of the ventricle".

For *Ambystoma mexicanum* and *Hynobius keyserlingii* KÖRNER (1938) describes veins situated on the atrium wall and opening direct into the right atrium. In the specimens of *Ambystoma mexicanum* Shaw examined by us these vessels are not recovered.

VIII. THE NERVES OF THE HEART

Francis (1934) in *Salamandra salamandra* L. notes the presence of some heart nerves: a fine anterior cardiac nerve running to the truncus arteriosus near the pulmonary arch, and one or more posterior cardiac nerves, which accompany the pulmonary vein to the heart.

Carlson (1905) for *Necturus maculatus* describes nerve cells and nerve fibres in bulbus cordis, sinus venosus, atrium and ventricle walls.

Körner (1938), too, describes nervous elements in many cases in the heart of the numerous Urodela examined by him.

We have taken much pains to perceive the course of nervous elements but have had no success. Nerve cells in the sinus venosus and ventricle walls and in the mesocardial ligament between the ventricle and the sinus venosus are perceived by us, but for a closer study of this material a special technique seems necessary to us.

IX. THE CAROTID LABYRINTHS

Own investigation

The peculiar round or oval bodies met with in the adult animals of *Salamandra maculosa* Laur. at the carotid arches, the so-called carotid labyrinths (carotid glands) do not develop before the last stages of metamorphosis (specimens nos 13, 14, etc.).

In younger larvae, where these bodies are not to be found, the situation from where these bodies develop, is the following. The original gill vein III splits at the caudal end of the cerato-branchial into a dorsal branch, the origin of the arteria carotis interna, and a ventral branch, the origin of the arteria carotis externa (fig. 20). The latter vessel runs over a large distance in cranial direction parallel with the carotid arch, so it is caudalward connected with the origin of the arteria carotis interna by a connecting vessel. The arteria carotis externa and the carotid arch are connected by one or two thin anastomoses hanging together in some larvae.

When studying the successive specimens it appears that these anastomoses always lie in a cranial-caudal direction closer to the opening of the arteria carotis externa into the gill vein III, which later becomes the basal part of the arteria carotis interna (fig. 20 and 23). This must be explained by the more intensive caudal movement of the ventral bloodvessel complex in respect to the dorsal complex, as described above, owing to which the connecting piece from the arteria carotis externa to the arteria carotis interna also moves in a more dorso-ventral position – sometimes showing bends – but also, in our opinion, undergoing a relative shortening.

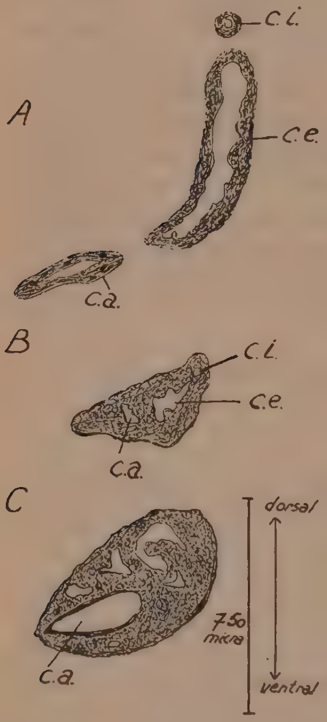

Fig. 27. Transverse sections through developing carotid labyrinths of *Salamandra maculosa* Laur. A. no 14. B. no 15. C. no 16. c.a., carotid arch; c.e., arteria carotis externa; c.i., arteria carotis interna.

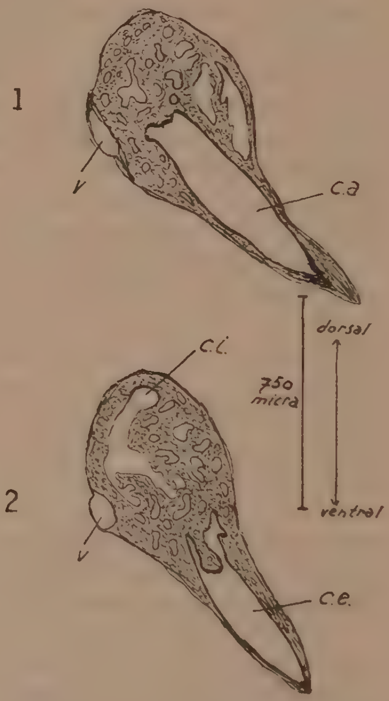

Fig. 28. Transverse sections through the carotid labyrinth of an adult *Salamandra maculosa* Laur. 1 = caudal; 2 = cranial. c.a., carotid arch; c.e., arteria carotis externa; c.i., arteria carotis interna; v., vein.

The anastomoses as well as the arteria carotis externa widen in proportion to the carotid arch.

In specimen no 12 and in older specimens we see especially at the connecting piece of the arteria carotis externa, but also at the carotid arch, bulges in the bloodvessels beginning to show themselves, which bulges lie in a proliferation of the walls of the blood vessels appearing at the same time.

This wall consists especially of polygonal cells with large nuclei. At the outside this thickened wall is covered with a fibrous layer while at the inside it is covered by an endothelium.

The connecting piece of the arteria carotis externa, connected ventrally by means of one or more anastomoses with the carotid arch, and dorsally connected with the arteria carotis interna, forms with these connections the origin of a simply constructed, long drawn-out carotid labyrinth with a central lumen (fig. 27). Already in specimen no 15 this complex is shorter and more compressed, and completely lying in a communal proliferation of the vessel-walls. The central cavity has become indistinct by the presence of many–also branchy–bulges, which bulges are mutually connected (fig. 27). The remainders of the caudal extensions of the carotid arch and gill vein III are reduced to narrow tubes.

In specimen no 16 the carotid labyrinth has obtained its characteristic shape. Into the oval body the carotid and the arteria carotis externa penetrate on the ventral side, while on the dorsal side the arteria carotis interna penetrates into it (fig. 27 and 28).

At the lumina of the ventrally penetrating vessels there appear connecting tubes making the central part of the body a spongy whole, which sponginess decreases in dorsal direction where the tubes unite themselves to an arteria carotis interna.

The remainders of the caudal extensions of the carotid arch and gill vein III are then wholly gone.

Histologically the construction of the carotid labyrinth is now that of the adult animals. The inside of the labyrinth wall consists of a thin endothelium on which are locally found thin layers of smooth muscular fibres. The chief mass of the wall consists of a thick tissue mass of polygonal cells with large nuclei round which lies a fibrous layer with connective tissue and smooth muscular elements forming the outer layer. In the completely adult animals the spongy construction has only grown more intensive. Cross-striped muscular elements are wholly missing. Ventro-laterally we now find a vein clearly lying against the wall of the carotid labyrinth.

In *Ambystoma mexicanum* Shaw carotid labyrinths are not present in neotenic and transformed animals.

Discussion

According to RUSCONI (1854) the carotid labyrinth in *Salamandra* should have arisen from the anastomoses between the arteria carotis externa and the carotid arch. Already BOAS (1883) contested this opinion and gave an extensive description of the development and the construction of the carotid labyrinth. In his Fig. 31, Taf. XXV (1882), the mutual connections of the anastomoses in the left part of this figure are represented too numerous. We even found that the presence of three anastomoses, as represented in the right half of the figure, is very rare indeed.

According to BOAS (1883) the carotid arch lying parallel to the arteria carotis externa should, both to the same extent, shape the origin of the carotid labyrinth by bulges. However, we are of opinion that the bulges arise especially from the arteria carotis externa, and to a less extent from the carotid arch; which is also perceivable in BOAS' Fig. 32, Taf. XXV (1882), but does not appear from the text.

MAURER (1888) supposes, referring to his observations on Anura, that also in Urodela epithelial elements should be connected with the forming of the carotid labyrinth, although he could not prove so from the Urodela that were at his disposal. We have taken much trouble to discover an epithelial layer as described by MAURER in all the specimens examined by us, but have not succeeded in it.

We want here to render our heartfelt thanks to Prof. Dr C. J. VAN DER KLAAUW, from the Government University of Leyden, for his directions and critical remarks concerning this investigation.

SUMMARY

I. The heart

Shape and positon of the heart. The changes in the shape of the heart during metamorphosis mainly consist of a cranial movement of the sinus venosus in respect to the atria and a lengthening of the longitudinal axis of the heart.

In the neotenic axolotl this shape has already been reached, so that the heart of these animals corresponds with the situation in the transformed animals.

A caudal movement in respect to the neighbouring skeleton can be proved. At first this caudal movement must be attributed to an intense growth of the heart as compared to the skeleton, in which growth, however, the cranial parts of the heart do not move in respect to the skeleton.

In *Salamandra maculosa* Laur. an absolute caudal movement is seen in the later stages of metamorphosis, which continues even after metamorphosis. In *Ambystoma mexicanum* Shaw, on the other hand, this caudal movement begins already before the phenomena of metamorphosis, so that in the neotenic animals the heart has already pretty far moved in a caudal direction; this movement continues during and after metamorphosis.

Sinus venosus. Besides the changes in the structure of the wall of the sinus venosus it is especially the formation of the big sinus valve which shows itself in the heart of *Salamandra maculosa* Laur. during metamorphosis.

This sinus valve originates in *Salamandra maculosa* Laur. as a side flap attached to the septum atriorum from the right part of the connective tissue border round the vena pulmonalis running across the dorsal wall of the sinus venosus. This border round the vena pulmonalis is connected with the septum atriorum, there where the vena pulmonalis opens into the left atrium to the left of the septum atriorum. By a caudally directed scooping out of its cranial part and by growth the sinus valve originates from the left part of the connective tissue border.

In *Ambystoma mexicanum* Shaw the connective tissue border is in young larvae much less developed. The sinus valve attains a much slighter development or may even be completely wanting.

Atria. In connection with the origin of the sinus valve as described by us it is doubtful whether KÖRNER's theory (1938) of the structure of the septum atriorum in lungless salamanders is correct.

The left part of the connective tissue border round the vena pulmonalis leads to the shaping of the vena pulmonalis funnel.

The septum atriorum is pierced by numerous openings arising before and during metamorphosis. From investigation it becomes probable that there is a connection between the appearance of these openings and the arising of muscular elements in the septum atriorum.

These openings in the septum atriorum are already present in neotenic *Ambystoma mexicanum* Shaw, but here as well as in the transformed animals they are fewer than in *Salamandra maculosa* Laur.

Ventriculus. In *Salamandra maculosa* Laur. we find in the atrio-ventricular opening as a rule one large dorsal valve, one large ventral valve, and a smaller right lateral one. A fourth left lateral valve may develop in the adult animals or is present as an endocardium ridge.

In *Ambystoma mexicanum* Shaw the ventricle is in young larvae surrounded by a thick epicardium layer, which is present to a smaller extent in neotenic animals and mostly disappears wholly in the transformed animals. In these animals we find two large valves in the atrio-ventricular opening, a dorsal valve and a ventral valve. Right laterally there may be present a slightly developed connective tissue ridge; only seldom we find a left lateral ridge.

Bulbus cordis. The bulbus cordis consists in a slightly spiral shaped tube, which, in its caudal part, possesses a ventral bend, owing to which this organ shows a great likeness to the conus arteriosus of *Ceratodus* (Boas, 1880 and 1882; Langer, 1894).

Although in the young larvae of *Ambystoma mexicanum* Shaw this spiral shape is less clearly perceptible than in neotenic animals, yet we think from the fact that it is strongly developed in *Salamandra maculosa* Laur., we may safely assume that Körner's opinion that this spiral should be of a secondary nature is not correct.

In the caudal part of the bulbus cordis we rather constantly find three valves. A fourth valve is more present in *Ambystoma mexicanum* Shaw than in *Salamandra maculosa* Laur.

The longitudinal ridge is in transverse sections higher in *Ambystoma mexicanum* Shaw than in *Salamandra maculosa* Laur.

The ridge corresponds with the three valves lying most cranially in the longitudinal row of valves in the conus of

Ceratodus (LANGER, 1894). For this reason it is fairly understandable that this ridge is only slightly spiral-shaped, as it corresponds with the cranial valves in the conus of *Ceratodus* only.

Besides the above mentioned cranial bulbus valve there are always three other cranial valves present.

The endocardium knobs in the cranial part of the bulbus cordis may correspond with rests of the second transverse row of valves in the conus of *Ceratodus*.

The cartilaginous bodies found in the cranial bulbus valves of *Salamandra maculosa* Laur. cannot be attributed to old age only, as KÖRNER (1938) asserts.

II. The truncus arteriosus and arterial arches

Truncus arteriosus. In young specimens of *Salamandra macucosa* Laur. the truncus septa are covered with thick endocardium layers disappearing during metamorphosis. In *Ambystoma mexilanum* Shaw the endocardium disappears during metamorphosis but here the septa are in transformed animals much thicker.

It is difficult to decide whether the cross-striped muscular layer round the truncus arteriosus belongs to the lymph heart or to the truncus itself.

A new nomenclature for the septa appeared desirable.

Arterial arches. In the larvae of *Salamandra maculosa* Laur. there arise four pairs of arterial arches from the truncus arteriosus. After the end of the metamorphosis either the third pair of arches or one arch in the third pair may disappear.

Especially the ventral parts of the arterial arches of *Salamandra maculosa* Laur. move together with the heart in a caudal direction early during metamorphosis.

The dorsal bloodvessel system does not move at all, or does so only to a small extent. Only the dorsal junction of the aorta roots is found to lie more caudally in older animals than in young larvae.

The ventral bloodvessel complex in *Ambystoma mexicanum* Shaw moves caudally before metamorphosis already.

In *Ambystoma mexicanum* Shaw four pairs of arterial arches are invariably present, the third pair having a smaller diameter in older animals.

In a few animals the pulmonary arch arises from the "third" arch exactly there where this leaves the truncus arteriosus. This situation makes a relation of these animals with *Siren* – as described by Boas (1882) – more likely.

Contrary to the finds of McMullen (1938) the arteria maxillaris externa in *Salamandra maculosa* Laur. and *Ambystoma mexicanum* Shaw is already present before metamorphosis.

III. The Pericardium, Lymph heart, Bloodvessels and Carotid labyrinth

The pericardium. In the pericardium we may also find a remainder of the ligamentum hepato-entericum in the adult *Salamandra maculosa* Laur. and *Ambystoma mexicanum* Shaw.

The central lymph heart. The muscular bands in the cranial part of the central lymph heart consist of cross-striped muscular fibres.

The bloodvessels of the heart. Along the dorsawall of the truncus arteriosus an artery is situated, ramifications of which penetrate into the truncus and bulbus walls. This bloodvessel is connected with the arteria carotis externa.

In *Salamandra maculosa* Laur. a heart vein runs from the cranial ventricle wall to the right duct of Cuvier. In *Ambystoma mexicanum* Shaw this bloodvessel is not clearly separated from the right duct of Cuvier.

Carotid labyrinth. The carotid labyrinth originates especially from bulges and proliferations on the wall of the arteria carotis externa, and partly from the same phenomena on the wall of the carotid arch. Epithelial elements (Maurer, 1888) do not appear to be connected with the formation of these bodies.

In *Ambystoma mexicanum* Shaw carotid labyrinths are not present.

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THE EFFECT OF CENTRIFUGAL FORCE UPON THE EGGS OF LIMNAEA STAGNALIS L.

BY

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INTRODUCTION

In recent years, our knowledge of the precocious chemodifferentiation in the so called mosaic eggs has improved considerably. The study of these eggs with modern histochemical methods has brought to light the presence of certain substances, which are at first distributed evenly throughout the egg protoplasm, but are localised into definite regions of the egg during the early stages of development.

The observations of Spek (1930–1934) on the "bipolar differentiation" of the eggs of diverse invertebrate animals and of Teleosts have shown that in these eggs, prior to or immediately after the beginning of cleavage, a rearrangement of the egg substances occurs, which leads to an accumulation of acid materials in the vegetative and of alkaline substances in the animal half of the egg. Recent researches (Ries & Gersch 1936, Raven 1938) prove that especially the accumulation of the acid albuminous yolk in the vegetative egg hemisphere is responsible for the occurrence of this difference in pH between the two hemispheres of the egg.

The observations of Ries & Gersch (1936) on *Aplysia* show that not only the pH, but also the rH of the egg protoplasm differs in different regions of the egg. Gersch & Ries (1937) have studied with the aid of vital dyes and indicators the arrangement of substances in the eggs of various marine animals, and the distribution of these substances during cleavage to particular regions of the embryo. Ries (1937) showed that vitamin C, glutathion and various enzymes (benzidine-peroxydase, indophenol-blue-oxydase, leucomethylene blue-oxydoreducase) in some marine eggs have a definite localisation in the uncleaved egg and become incorporated into particular blastomeres during cleavage.

In the light of these facts, it seems reasonable to suppose that these substances have something to do with the determination of the cells. As a matter of fact, RIES (1939) has shown that in the Ascidian egg the differentiation of muscle cells is dependent upon the presence of a special protoplasm, which is characterized by its riches in certain oxydases and peroxydases. In *Tubifex* the pole plasms, which determine the differentiation of the embryo, as is shown by the experiments of PENNERS (1924–25), are very rich in indophenolblue-oxydase too (LEHMANN 1941*a*). On the other hand, it would be premature to attribute to these substances, which can be detected with our present histochemical methods, the value of specific organ-forming substances. In fact, this notion of organ-forming substances has lost, in recent years, something of its positiveness. More and more, it has been made clear that the assumption of a specific substance, being responsible for the development of the cells, into which it has become incorporated, to some special organ of the embryo, is rather simplistic. The determination of the cell appears to depend on an equilibrium of the substances it contains; not the presence of a single substance, but rather the quantitative and spatial relation of various substances is determinative. So PELTRERA (1940) concludes from his experiments on the eggs of *Aplysia* that "con tutta probabilità, la complicata architettura ooplasmatica sia in queste uova sede di un complesso sistema di equilibrî istochimici, legati ad ossidasi, riduttasi, acido ascorbico, glutatione ed altre sostanze, che non possono venir turbati, senza che ciò influisca sull'armonia dei processi dello sviluppo". It is noteworthy that all these substances play a part in cell metabolism; their primary action seems to affect, therefore, the metabolic processes of the cell.

Little is known about the factors, which are responsible for the localisation of the egg substances in their definitive positions. The remarkable fact that in some eggs after abnormal stratification of the egg protoplasm by centrifuging a redistribution of the egg substances occurs, which may lead to a restoration of the normal arrangement of materials (RAVEN 1938, PELTRERA 1940), proves that these factors reside in those parts of the egg protoplasm, which resist the displacing action of centrifugation. They may correspond, therefore, to the factors determining the polarity and bilaterality of the egg; probably, they are located in the cortical layer of the egg.

As a matter of fact, MOTOMURA (1935) has shown that in the eggs of Amphibia and Echinoderms the cortical cytoplasm is not displaced by moderate centrifuging. This is confirmed, as regards the "cortical field" in the Amphibian egg, by the experiments of PASTEELS (1940). The action of cortical factors upon the distribution of the egg substances is demonstrated well in the experiments of LEHMANN (1940, 1941*b*): when the uncleaved eggs of *Tubifex* are centrifuged at an early stage of development, the pole plasms accumulate under the egg cortex in their normal positions with respect to the original polarity of the egg. As for the nature of these cortical factors, very little is known; we may quote in this respect the opinion of SPEK (1930), who ascribes the "bipolar differentiation" of the egg of *Nereis* to differences in the permeability of the egg cortex; in consequence of a different penetration of ions an electrical field is established, resulting in the migration of the colloid particles of the protoplasm to the poles of the egg ("kataphoresis in the living cell", after SPEK).

Experiments, in which the normal arrangement of egg substances has been destroyed by means of centrifugal force, have furnished an important contribution to the analysis of the development of mosaic-eggs. The observation that from such eggs in many cases (e.g. in Polychaetes and Molluscs) normal larvae develop, regardless of the distribution of the visible egg materials, has lead to the prevailing opinion that these substances (particularly fat and albuminous yolk) play no part in the determination of the cells, but are raw materials only, which are consumed as food during the development of the embryo. They were contrasted, therefore, with the organ-forming substances proper, which cannot be displaced without disturbing the normal course of development.

Such a view, however, does not agree with our conclusion that the determination of the cells depends on the physical and chemical equilibrium of all the substances it contains, primarily affecting the metabolic processes of the cell. According to this view, the sharp line of demarcation between "organ-forming substances" and "raw materials" cannot be maintained. Moreover, recent experiments have shown that in many instances the yolk materials of the egg play an important part in determination (cf. LEHMANN 1938). Lastly, it has been found by one of us (RAVEN 1938) that the development of centrifuged eggs of *Nereis* and *Chaetopterus* in a large percentage of cases is abnormal, so that some doubts have arisen as to the accuracy of earlier experiments, and the exactness of their interpretation. Therefore, we have tried to gain a better insight into the problems of the development of centrifuged eggs, using the eggs of *Limnaea stagnalis*.

Centrifuge experiments with the eggs of fresh water Pulmonates (*Physa ancillaria* and *Lymnaea catascopium*) have been made by CONKLIN (1910). The eggs showed after centrifugation a stratification into three zones: a cap of "gray substance" at the centripetal end, a clear zone, and a layer of "yellow substance" at the centrifugal end of the egg. This stratification may bear any relation to the original axis of polarity. At further development, this abnormal arrangement of the visible materials of the egg is, in the main, preserved; nevertheless, in a large percentage of cases normal young snails develop, particularly, if the eggs were centrifuged before or immediately after maturation. CONKLIN concluded, therefore, that the gray and yellow substances are mere inclusions in the protoplasm, and that they neither are essential to development.

The observations of CONKLIN were made on living eggs only. The study of whole eggs, however, can give us but a superficial impression of the distribution of egg materials. A better insight into the developmental processes in the centrifuged eggs may be gained from the study of sections. It may reveal finer details of arrangement of the egg materials, which are indispensable for a full understanding of development. Moreover, it appeared worth while to study the distribution of other substances, not visible in the untreated egg, but demonstrable with special histochemical methods.

MATERIAL AND METHODS

Adult *Limnaea stagnalis* were obtained from ditches near Utrecht. They were kept in large numbers in glass aquaria, containing ± 30 l of tap water; no submerged plants were added, the snails being fed with lettuce. Under these circumstances they produce, as a rule, no egg-masses. To obtain eggs, some floating aquatic plants (e.g. *Hydrocharis*) are added. Now, after a lapse of ± 3 hours large numbers of egg-masses are produced. Evidently, the presence of these plants stimulates the snails to deposit their eggs. The nature of this stimulus is not yet known to us; preliminary experiments have shown, however, that it is, probably, not chemical. In this way, it is possible to have the egg production in hand, and to obtain the egg-masses at will precisely at the moment they are needed.

It should be noted that many egg-masses obtained in this way contain a large number of abnormal eggs. These eggs are larger than normal ones; in many cases they do not cleave, in other eggs development stops at an early stage. In such egg-masses usually some capsules contain more than one egg; sometimes, 20 or more eggs are enclosed in one capsule. As a rule, the egg-masses, which are deposited promptly (i.e. within 3–6 hours) after the application of the above-named stimulus, are normal; with increase of the period of latency the egg-masses contain more abnormal eggs, while egg-masses deposited after more than 12 hours nearly always show 100% mortality. Of course, only the firstmentioned egg-masses were selected for the experiments.

The eggs were centrifuged in their capsules by means of an electric centrifuge; as a rule, they were centrifuged during 5 minutes at a velocity of 3800 revolutions per minute, giving a centrifugal pressure of 1860 × gravity. In this way, a distinct stratification of the eggs is effectuated, as described below.

For fixation of the eggs, and for the execution of the histochemical reactions, it proved necessary to deliver the eggs from their capsules. To this end, the following method has been employed: the common jelly mass is removed as far as possible, then the individual egg capsules are placed upon a dry glass plate. After a few minutes, the capsules, originally resistant and elastic, are somewhat wrinkled in consequence of drying; now it is easy to prick the capsule with a pointed needle, and get out the egg. Out of their capsules, the eggs may survive for some days in tap water; they may undergo cleavage, and develop into a gastrula; then development stops and the eggs die.

As for the technical details of the histochemical reactions employed by us, we may refer to LISON (1936) and to the papers of RIES.

THE DEVELOPMENT OF CENTRIFUGED EGGS

Fig. 1 gives a graphic representation of the effect of centrifuging in relation to time. At the abscissae the time is represented. The uncleaved stage of *Limnaea stagnalis* lasts 4–5 hours (at a temperature of ± 20°). The first polar body is extruded 60–80 minutes after the egg is laid; the second polar body is formed about one hour after the first; after another 2–2½ hours cleavage begins. The ordinates represent the "total mortality",

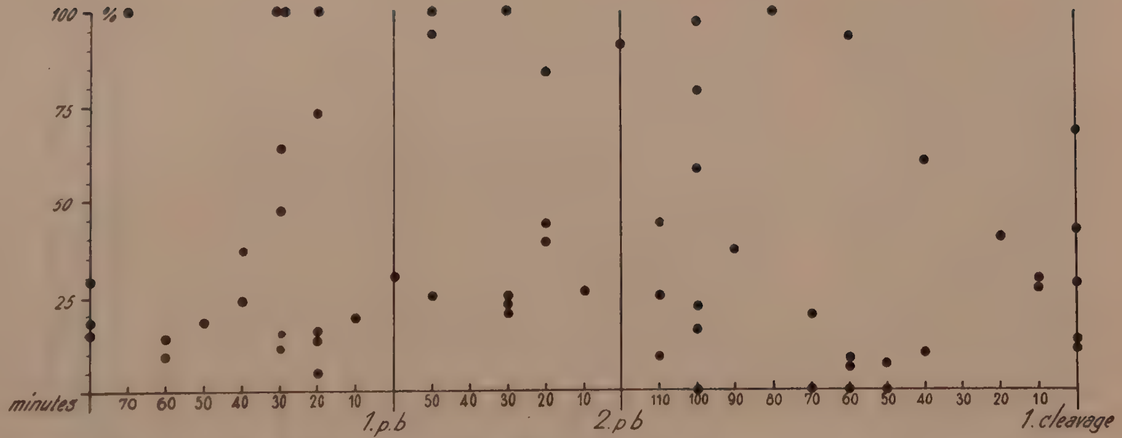


Fig. 1. Graph showing mortality of *Limnaea* eggs after centrifugation at different moments during the uncleaved stage.

Abscissae: time in minutes before first polar body (1.p.b.), before second polar body (2.p.b.) and before first cleavage (1.cleav.). Ordinates: percentage mortality. Each point corresponds to one egg-mass.

i.e. the percentage of eggs, from which no normal young snails hatched, either owing to precocious death of the embryo, or because development was abnormal.

63 Egg-masses, containing 3193 eggs, are included in the graph; all were centrifuged between egg deposition and first cleavage. The mean rate of mortality is 32%. As the figure shows, the rate of mortality varies very much (from 0% to 100%); there is no definite increase in mortality at the end of the uncleaved stage. We may divide the uncleaved stage into four nearly equal periods, viz.: 1°. from egg deposition to first polar body formation, 2°. from first to second polar body, 3°. one hour after second polar body, 4°. one hour before first cleavage, and determine the total mortality in these periods (Table 1).

TABLE 1

Periods	Eggs	Dead or abnormal	%
I. Deposition to 1.p.b.	1090	321	29
II. 1. to 2.p.b.	713	281	39
III. 1h. after 2.p.b.	667	228	34
IV. 1h. before 1.cleav.	723	187	26

The table shows that the rate of mortality shows some difference in these four periods, being highest during maturation, lower before and after this period; the differences are, however, small, and it is not certain that they have a real value.

In comparison with this, 8 normal egg-masses, containing 458 eggs, showed a mean mortality of 23%, varying between 5% and 50%.

Our results show that the injurious effects of centrifuging upon development are small, and not very dependent upon the stage of operation. Perhaps centrifuging is most injurious during polar body formation. It can be stated with certainty, however, that there is no increase in mortality up to the time of first cleavage; rather, the reverse is true. This is in contradiction with the conclusions of Conklin, who saw an increase in the injurious effects of centrifuging from the time of the first maturation to that of the first cleavage. The tables given by Conklin show, however, that the number of his experiments is far too small to justify such a conclusion. With *Limnaea catasco-*

pium, only 3 egg-masses were centrifuged after the beginning of maturation; with *Physa ancillaria* the number of experiments is larger, but in most cases the exact stage of the eggs at the time of centrifuging and the precise number of normal as compared with abnormal embryos is not recorded; moreover, the length of time during which the eggs were centrifuged was varied considerably, which makes a comparison of the results difficult.

Conklin's experiments were repeated and extended by Clement (1938), using *Physa heterostropha*. This author states that "the effects of centrifuging .... are least injurious just after the completion of maturation and most injurious just before the first cleavage". Though Clement's eggs were centrifuged for 10 minutes at 6300 × gravity, and his experiments are, therefore, not directly comparable with ours, his table 3 shows that the number of his experiments is far too small: only 379 eggs form the basis of his conclusion. We know by experience that such a small number of experiments may lead to misleading conclusions.

THE STRUCTURE OF CENTRIFUGED EGGS

The zones of substances, as seen in eggs centrifuged at different moments during the uncleaved stage, are shown in fig. 2. The

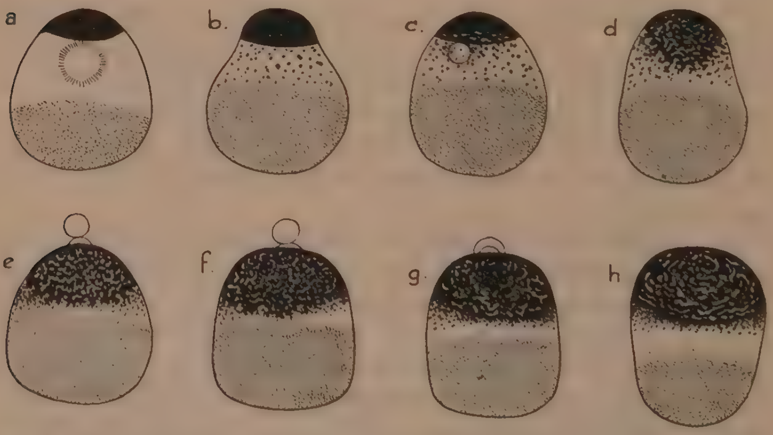


Fig. 2. Eggs of *Limnaea stagnalis*, centrifuged at different moments during the uncleaved stage. *a.* 20 minutes before formation of first polar body; *b.* 15 minutes; *c.* 35 minutes after first polar body; *d.* 10 minutes; *e.* 50 minutes; *f.* 80 minutes; *g.* 95 minutes; *h.* 110 minutes after formation of second polar body.

first of these was centrifuged 20 minutes before the extrusion of the first polar body, the others successively later; the last of the series was centrifuged shortly before the beginning of cleavage.

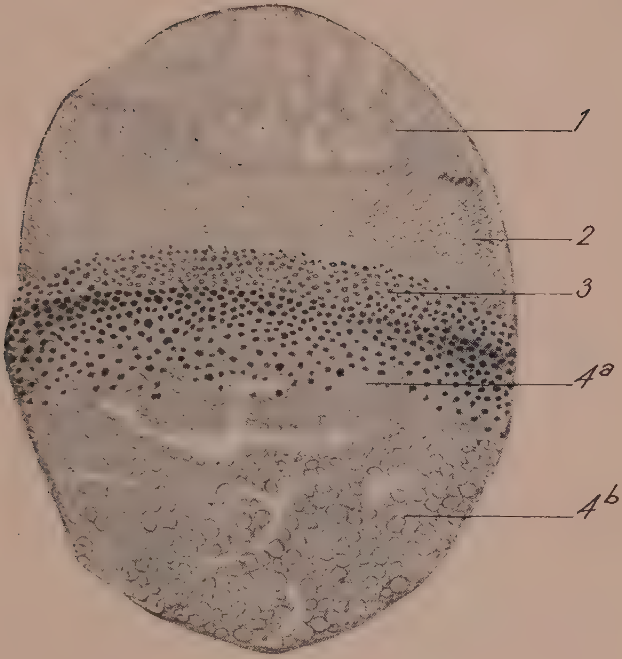
The figure shows that eggs centrifuged before maturation have a distinct stratification into 3 zones: a centripetal zone, dark in transmitted light, white in reflected light, corresponding to Conklin's "gray substance"; a centrifugal zone, somewhat less dense in transmitted light, yellow in reflected light, Conklin's "yellow substance"; and an intermediate zone of clear protoplasm, often showing a radiating aster, indicating the position of the maturation spindle. In the eggs centrifuged before maturation, this zone is rather broad, and almost perfectly transparent; it is sharply separated from the gray and the yellow substance.

In eggs centrifuged at a later stage with the same centrifugal force, the aspect is different. In the first place, the separation of the substances is less complete; the clear zone is less transparent, and contains a large number of yolk granules and fat droplets. At the same time, the clear zone is narrower; in the eggs centrifuged 50 minutes after the formation of the second polar body it is hardly visible, the gray and yellow materials nearly composing the whole of the egg. Then, up to the end of the uncleaved stage, the substances are separated better again. This variation in the rate of stratification is an indication of important changes in the physical state of the egg protoplasm; it may be due to increasing viscosity of the protoplasm, attaining its maximum about one hour after the formation of the second polar body, then decreasing again in some degree. On the other hand, a change in the specific gravities of the egg substances during development might be responsible for the effect. The occurrence of such a change was concluded by Conklin from his observations on the rapidity of orientation of centrifuged eggs: until the first maturation, these eggs orient rapidly, with the yellow pole down; after maturation, the eggs orient more slowly.

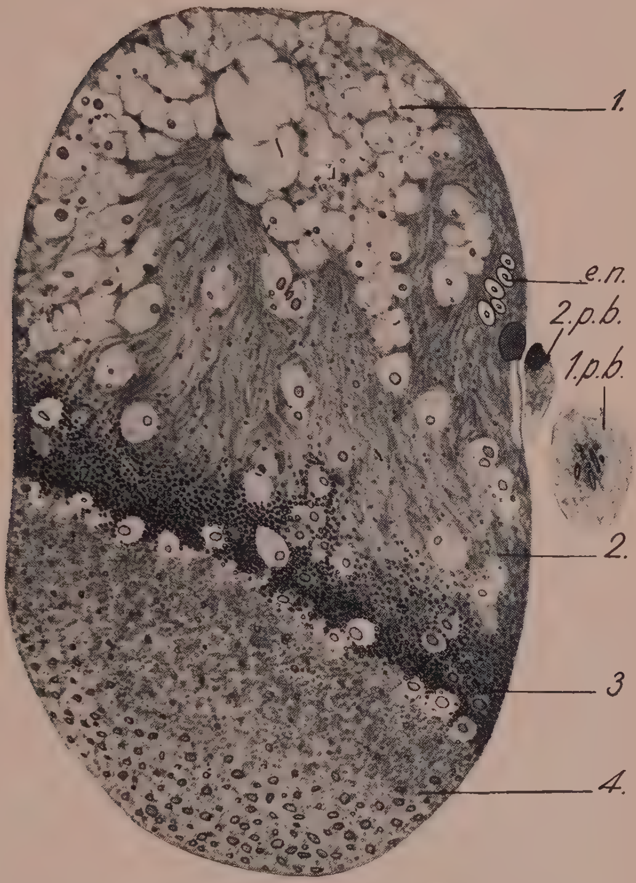
Secondly, the figure shows that the relative proportions of gray, clear and yellow substances undergo considerable changes during the uncleaved stage of the egg. At first, the gray substance composes only a small cap of the egg; it is very compact, and sharply separated from the clear substance. After maturation it increases in quantity, and becomes vacuolar in appearance, consisting of many small droplets loosely packed; at the end of the uncleaved period it constitutes about one-half of the entire egg. On the contrary, the yellow substance, which at first composes about one-half of the egg, decreases during development, and just before the first cleavage forms only about one-quarter of the egg. These changes are accompanied by a difference in shape of the entire egg. At first, this is pear-shaped with point directed upward (centripetally); at later stages, the centripetal half of the egg is larger in transverse diameter than the centrifugal half.

These changes in the relative proportions of the egg substances were observed already by CONKLIN (1910) and by CLEMENT (1938). CONKLIN explains them by a dissolution of the yellow substance, and its transformation into clear and gray substance. Another interpretation of the facts is given by CLEMENT: the increase in quantity of the gray material is due to an accumulation of large vacuoles in this region; these are probably watery in composition. They arise by transformation of unpigmented granules; at first, these granules have a great specific gravity, and segregate, therefore, at the heavy pole of eggs centrifuged just after laying. Through a swelling process, they transform into the vacuoles; now, their specific gravity is so lessened that they come to occupy the light end of the centrifuged egg. At the same time, the volume of the egg increases through an absorption of water; this increase is roughly equivalent to the estimated volume of the vacuoles formed in the egg.

In *Limnaea*, the increase in quantity of the gray material is accompanied by the appearance of a large number of vacuoles, too. In eggs centrifuged before maturation, this part of the egg (zone 1) in sections is sharply separated from the clear protoplasm (zone 2) (plate III); in eggs centrifuged after maturation, zone 1 shows a vacuolar appearance and a gradual transition into zone 2 (plate IV). When these eggs are treated with Sudan III (cf. below), the contents of the vacuoles remains unstained; in the meshes between the vacuoles, however, small fat droplets are accumulated, which show a bright red coloration. This proves, that in *Limnaea*, too, these vacuoles are, probably, watery in composition. As will be described below, the origin of these vacuoles in *Limnaea* is comparable to that in *Physa*; they arise by transformation of the γ-granules (cf. below p. 268). With the



Egg of *Limnaea stagnalis*, centrifuged immediately after deposition and fixed shortly afterwards (FS 1).
1. Fat zone. 2. Zone of hyaloplasm. 3. Zone of α-granules. 4. Zone of albuminous yolk (*a* and *b*: the two parts of it).



Egg of *Limnaea stagnalis*, centrifuged 15 minutes after formation of second polar body and fixed shortly afterwards (DE 1). 1. Vacuolated fat zone. 2. Hyaloplasm. 3. Layer of α-granules. 4. Albuminous yolk. *e.n.* Karyomeres of egg nucleus. *p.b.* polar bodies.

centrifugal force applied usually, these granules in the eggs centrifuged before maturation are accumulated in the centrifugal part of the egg, scattered between the β-granules of the albuminous yolk. With stronger centrifugation (15 min. at 4500 revolutions per minute) they segregate, however, in the most centrifugal part of the egg, as in the eggs of *Physa* in the experiments of CLEMENT.

Plate III is a section of an egg centrifuged immediately after deposition. The egg protoplasm shows a stratification into four zones. The first of these, at the centripetal end, corresponds to the gray substance visible in unsectioned eggs; the second to the zone of clear protoplasm. Then follows a narrow layer of small granules, not visible in the living egg; lastly, a thick mass of large granules, which composes the centrifugal end of the egg.

In eggs centrifuged after maturation, these same four zones can be distinguished (plate IV). However, as noted above, in such eggs there is no sharp boundary between zones 1 and 2.

Concerning the nature of the substances forming these four zones of the centrifuged egg, the following observations were made. Centrifuged eggs were fixed in formalin, then treated with various fat stains (Sudan III, Scharlach). In these eggs, only zone 1 takes the stain, and shows a bright red coloration (fig. 3). As this zone, furthermore, blackens with osmic acid, it may be concluded that it consists, mainly, of fatty materials, at least in eggs centrifuged before maturation. As the reaction of LIEBERMANN-BURCHARDT-SCHULTZE is negative, whereas with the reaction of LORRAIN SMITH this zone shows a light red color, it seems that it contains especially trioleine, or other unsaturated glycerides (cf. LISON 1936, p. 203).

In paraffin sections of eggs centrifuged before maturation zone 1 is nearly empty, the fat being dissolved during the preparation of the sections. At the periphery, a narrow band of protoplasm is left, and some fine protoplasmic threads may cross the empty space (plate III). In eggs centrifuged after maturation, this zone is vacuolar in appearance, containing many nearly round vacuoles enclosed in a protoplasmic network (plate IV). The vacuoles are accumulated at the centripetal end, becoming less numerous as zone 1 passes into zone 2. Most of the vacuoles contain a rather large granule, staining black with iron hematoxylin, and red with azan; probably, this is the γ-granule, which has given rise to the vacuole in the manner described below

(p. 268). As noted above, these vacuoles are, probably, watery in composition, the fat droplets lying in these eggs in the meshes between the vacuoles.

Zone 2 in paraffin sections consists of a rather dense protoplasm, being somewhat filamentous in appearance in eggs fixed in Bouin's fluid. In most eggs, it contains the egg-nucleus or the maturation spindle (plates IV, V, VI), though in some cases this may lie in the third, of even partly in the fourth zone. In eggs centrifuged before maturation zone 2 is sharply separated from the adjacent zones, and nearly devoid of visible inclusions; it may contain some scattered yolk granules only. After maturation, as stated above, its separation from zone 1 is not sharp; scattered vacuoles may be found in the major part of zone 2 (plate IV).

It could be demonstrated histochemically that glutathion in the centrifuged eggs is accumulated in zone 2 (fig. 3). This corresponds to its distribution in normal eggs, where it surrounds the nucleus, as will be shown in another paper.

Zone 3 is a narrow band of very small granules (α-granules), staining violet blue with iron hematoxylin, and orange red with azan. It corresponds in situation and appearance to the third zone in the egg of *Physa*, after CLEMENT (1938). In *Limnaea*, too, these granules stain selectively with acid fuchsin in sections prepared according to the Altmann technique for mitochondria; it is probable, therefore, that they are mitochondria. As, however, these granules cannot be demonstrated in sections of eggs, fixed in Champy and stained after Benda, some doubt as to their nature remains. Therefore, we prefer to call them α-granules.

The histochemical reactions employed by us show that this zone of α-granules constitutes a very important part of the egg protoplasm. In it are accumulated the indophenol-blue-oxydase and benzidine-peroxydase (fig. 3); the glycogen of the egg is concentrated in this zone, too. The reaction of GIROUD & LEBLOND for the detection of vitamin C furnished uncertain results only; however, in some cases a vestigial ring of small black granules, corresponding in site to zone 3, could be made out with some difficulty. So it appears that most of the physiologically active substances of the egg protoplasm are bound to this zone of α-granules.

Zone 4, composing the centrifugal part of the egg, consists of a dense mass of rather large granules (β-granules). In sections stained with iron hematoxylin and eosin, these granules are red;

after staining with azan they are dark blue. Scattered among the β-granules are very large γ-granules, staining deep black with iron hematoxylin, and orange red with azan; in sections stained with iron hematoxylin and eosin some of them have a speckled appearance, being partly red and partly black.

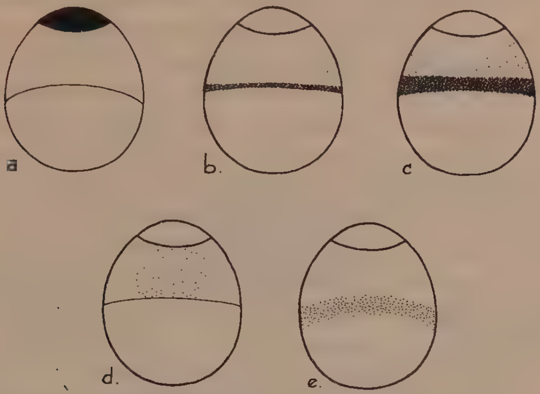


Fig. 3. Histochemical reactions with centrifuged eggs of *Limnaea stagnalis*. Distribution of *a.* fat. *b.* benzidine peroxydase. *c.* indophenol blue oxydase. *d.* glutathion. *e.* glycogen.

In most eggs, the fourth zone can be subdivided into two parts: a denser layer along zone 3 (zone 4*a*), and a centrifugal cap, where the distribution of the granules is less dense (4*b*).

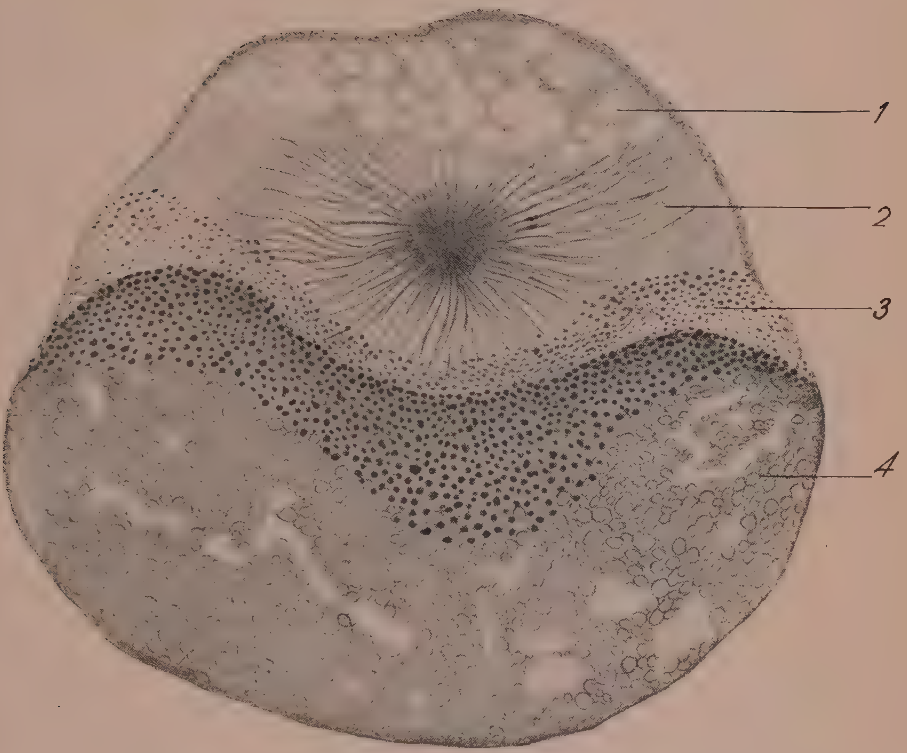
Evidently, the β-granules represent the albuminous yolk of the egg; with Millon's reagens they stain red. We agree with Clement that the opinion of Gatenby (1919), who considered them to be mitochondria, cannot be maintained. In the living egg, this mass of yolk is yellow in color; we could not yet determine whether this color is due to pigment granules scattered within the yolk mass, or to a coloration of the yolk granules themselves. With the highest magnifications used, no distinct pigment granules could be observed between the yolk granules. As the yellow pigment is highly resistant against strong acids, but is discolored by oxydants, like Cl_2, it belongs, probably, to the group of melanines.

The γ-granules are to be considered as a special element, destined to give rise to vacuoles by an absorbtion of water. As noted above (p. 265), before maturation these γ-granules have a great specific gravity; after strong centrifugation they are segregated at the centrifugal end of the egg. With the centrifugal force applied usually, they may be found in more centripetal regions of zone 4.

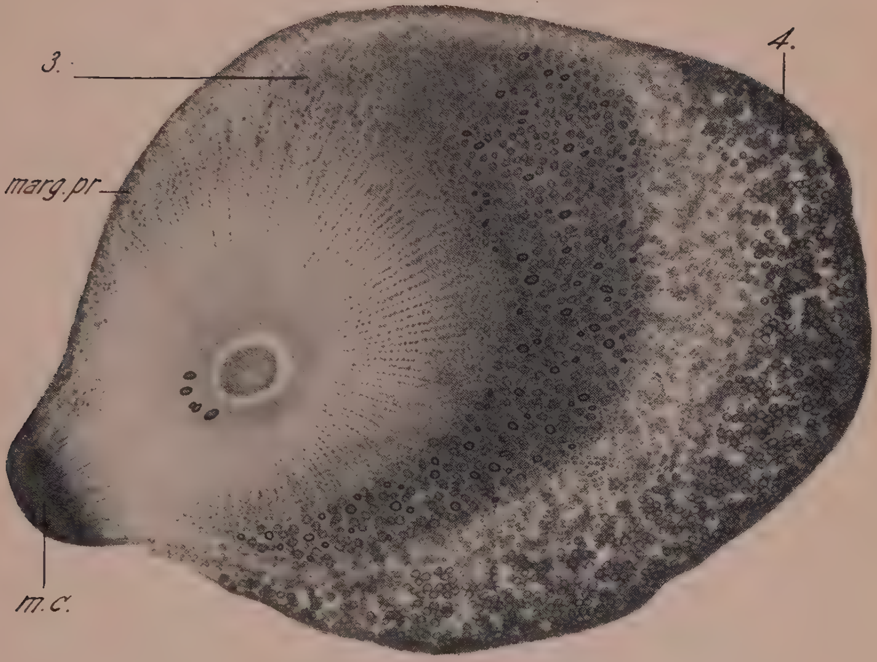
In sections of eggs centrifuged after maturation, part of the γ-granules may be surrounded by a clear space; probably, this indicates the beginning formation of vacuoles originating from these granules, as admitted by CLEMENT. Often, these young vacuoles are heaped up at the boundary between zones 3 and 4 (plate IV). As the volume of these increases and their specific gravity is decreasing accordingly, they are accumulated more and more at the centripetal end of the egg. So, in such eggs, a gradual transition between γ-granules and large vacuoles, from one end of the egg to the other, may be seen (plate IV). It should be noted, that the formation of the vacuoles is not accompanied by the disappearance of the γ-granules; on the contrary, even in the largest vacuoles the granule is retained. Thus, the vacuoles do not arise from the granules by a process of liquefaction or swelling; rather, the γ-granules seem to attract water from the neighboring protoplasm and, in that way, are surrounded by a mantle of fluid. Of course, it is possible that a part of the substance of the granules is dissolved during the formation of the vacuoles, or that a swelling of the granules occurs; as a matter of fact, however, no regular differences in diameter between the original γ-granules and those contained in the vacuoles could be demonstrated. The fact that the granules are not thrown out of the vacuoles during centrifuging, but move together with the surrounding fluid to the centripetal end of the egg, might be an indication, however, that some swelling process and a corresponding decrease in the specific gravity of the granules has occurred.

As to the nature of the γ-granules, nothing definite could be made out; from their staining reactions, however, it seems probable that they are albuminous in nature.

It has been found by one of us that in the eggs of *Nereis*, *Chaetopterus* and *Aplysia* the albuminous yolk shows an acid reaction, when treated with vital dyes, whereas alkaline substances are accumulated in the hyaloplasm or fat zone of centrifuged eggs (RAVEN 1938). In *Limnaea*, such differences in pH of the egg substances could not be demonstrated. When treated with vital dyes (neutral red, nile blue chlorhydrate, brilliant cresyl violet), the eggs are rather weakly colored; no



Egg of *Limnaea stagnalis*, centrifuged just after laying and fixed 20 minutes later (FS 1). Beginning derangement of the stratification.
1–4. The 4 zones of the egg.



Egg of *Limnaea stagnalis,* centrifuged just after laying and fixed one hour later (AO 1). Derangement of the layers by maturation aster. 3. Layer of α-granules. 4. Albumen zone. *m.c.* Maturation cone. *marg.pr.* marginal layer of protoplasm.

color differences, ascribable to variations in pH in the egg, were observed. Also, in normal eggs of *Limnaea* no "bipolar differentation" in the sence of Spek occurs, as will be shown in another contribution.

THE FATE OF THE DISPLACED SUBSTANCES

By tracing the development of single eggs, centrifuged just after egg deposition, considerable changes in the distribution of the egg substances can be observed (fig. 4). Till maturation the position of the displaced fatty and albuminous materials remains unchanged. Then, with the beginning of the first maturation division, protoplasmic currents occur, directed at the site of polar body formation. Streams of fat droplets and yolk granules flow through the zone of clear protoplasm. The boundaries between the three visible zones of the egg loose their sharpness, fat droplets and albumen granules penetrate into the plasm zone, that becomes narrower and narrower. At last, this zone is wholly absorbed by the two adjacent zones, progressing from both sides and meeting in the middle. After this, the spreading of the egg inclusions continues, leading to an interpenetration of both substances.

These observations show that the egg substances, which are displaced by centrifugation, do not remain in their positions, but are redistributed over the egg,

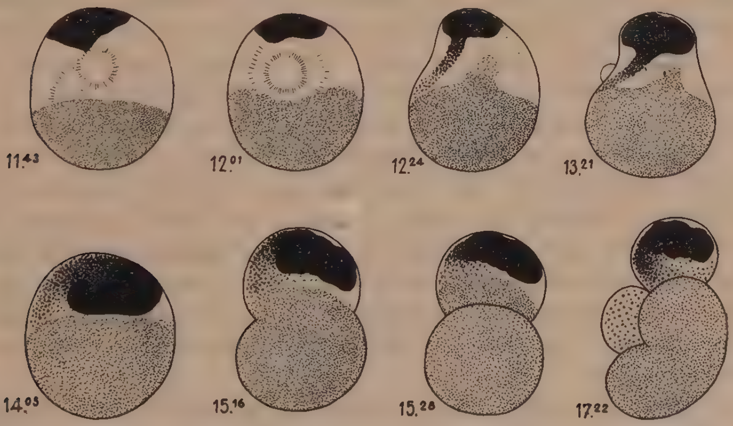


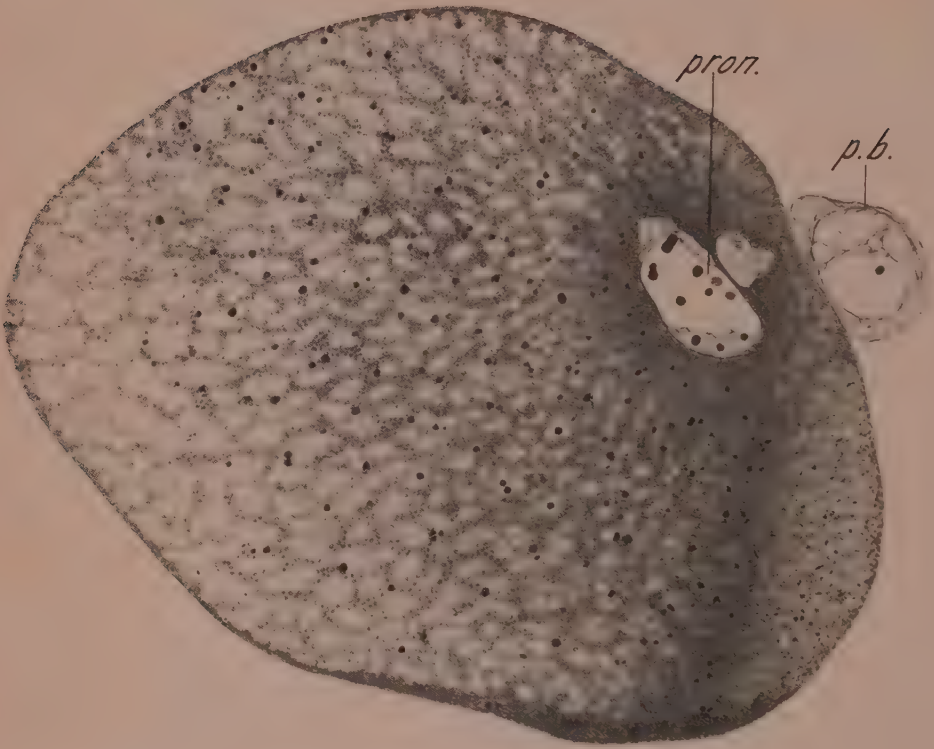
Fig. 4. The distribution of substances in a centrifuged egg of *Limnaea stagnalis* during further development of the egg (G I).

tending to a restoration of their normal arrangement. They are confirmed by other experiments, in which the distribution of special substances (enzymes, glutathion) was studied at different times after centrifugation; it could be demonstrated that these substances, too, in a relatively short time are redispersed over the egg. Furthermore, one can follow this process in sections of eggs, centrifuged before maturation, and fixed at regular intervals.

Plate V is a section of an egg, centrifuged just after laying and fixed 20 minutes later. The four zones of substances are distinct. In the plasm zone an aster is to be seen; it forms one of the ends of the maturation spindle, which is not included in the section. In this region the first sign of a derangement of the stratification can be observed; zone 3, and to a lesser extent also zone 4, show an indentation corresponding to the extension of the aster. The α-granules, originally forming this part of zone 3, may be seen lying somewhat deeper, between the albumen granules of zone 4. It appears, thus, that these α-granules were pushed aside and displaced by the extension of the astral rays.

Plate VI is a section of an egg, centrifuged just after laying and fixed one hour later, during the formation of the first polar body. The maturation spindle is sectioned nearly longitudinally. Its distal pole is lying in a conical prominence of the egg, the beginning of the first polar body. At the other extremity of the spindle, a large aster is formed, extending through the plasm zone of the egg. Near this spindle-pole, a couple of anaphase chromosomes is visible. With the exception of the fat zone, which is not included in the section, the layers of substances are distinct; but their original orientation has changed considerably. There is no longer a sharp boundary between zones 3 and 4; an intermingling of α- and β-granules has taken place at a large extent. Furthermore, the boundary-lines between the zones are no longer straight; the zones 3 and 4 are curved around the centre of the aster. This suggests a displacing action of the aster upon the egg materials forming these zones. As a matter of fact, the astral rays penetrate somewhat into zone 3; in this region, the α-granules are arranged in rows, lying in the spaces between the astral rays.

It should be noted that the most peripheral layer of the egg does not share in the stratification of the egg, a fact, which is very clear in this section. It consists of a dense protoplasm,



Egg of *Limnaea stagnalis*, centrifuged just after laying and fixed 4 hours later (AO v). Readjustment of the egg substances nearly completed. *Pron.* pronuclei in prophase. *P.b.* polar bodies.

staining blue in azan, which has a nearly equal thickness everywhere, with the exception of the maturation cone, where it has thickened considerably.

In eggs of this same batch, fixed 80, 120 and 210 minutes after centrifugation, respectively, the gradual readjustment of the egg contents could be followed. The stratification becomes less and less distinct; the intermingling of the egg substances leads to a nearly total disappearance of the former zones. The last eggs of this batch, fixed 4 hours after centrifuging, i.e. 10 minutes before the beginning of cleavage, show a nearly homogeneous egg protoplasm (plate VII). A dark band, traversing the egg from the region of the animal pole to a point at the side is perhaps a last indication of the original stratification of the egg. The protoplasm shows an alveolar structure; the various granules are distributed nearly equally throughout the egg.

So we may conclude, that in eggs centrifuged before maturation, a nearly normal distribution of substances has been restored before the beginning of cleavage. It is, therefore, not astonishing, that such eggs develop normally.

How is it, however, when we consider the distribution of substances in eggs centrifuged shortly before the first cleavage? We may expect, that in these eggs, too, the formation of spindles and asters and the protoplasmic currents accompanying the cleavage divisions will lead to a derangement of the original stratification and an intermingling of the egg substances. On the other hand, it might be expected, that the formation of the cleavage planes will stop a further interchange of substances between the cells and obstruct, therefore, the readjustment of the egg substances. As we have seen, however, such eggs may develop normally in a large percentage of cases.

Though we have not yet extensively studied the development of eggs centrifuged shortly before cleavage, some of our observations may throw some light on this problem.

Fig. 5 shows some eggs, centrifuged shortly before cleavage and fixed at various cleavage-stages; they were treated with Scharlach. Fig. 5*b* is an egg, fixed at the 8-cell stage; the fatty materials are heaped up in the macromeres in the neighborhood of the vegetative pole of the egg. Small fat droplets, scattered throughout the protoplasm of the micromeres and of the animal part of the macromeres, probably have been displaced during

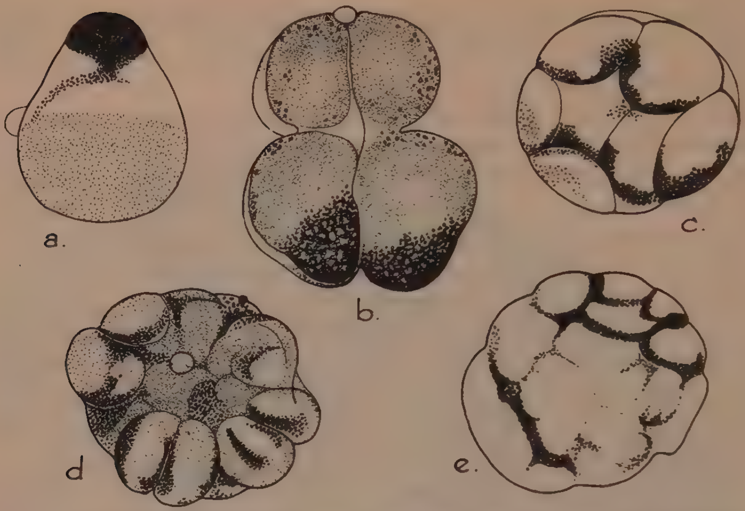


Fig. 5. Centrifuged eggs of *Limnaea*, stained with Scharlach. Distribution of fat during further development.

the first cleavage divisions. Fig. 5*c–e* show 3 eggs at a later stage of cleavage. The fatty materials are no longer accumulated in a definite mass at the surface of the egg, but are distributed over many cells; in the latter, they extend mainly along the cleavage furrows. This picture is very suggestive as to the manner, in which the redistribution of the fat substances takes place; probably, they are drawn out along the cleavage furrows, when these are cutting through the egg.

In this manner, the fat is dispersed over a larger region of the embryo; many of the cells of the embryo obtain a part of it. In other cells, however, no or only very little fat is included; in this way, therefore, no equal distribution of materials can be attained. However, in the blastula stage another process occurs. During cleavage, the fat droplets remain in a superficial position within the cells; now, they retire to deeper parts, where the cells of the blastula extend to the centre of the egg with conical prominences. It is, therefore, very difficult to determine precisely the position of the fatty materials, and the processes occurring in the central part of the embryo. However, some 2 days later, with the formation of the trochophore stage of development, it is easier again to demonstrate the fat droplets within the embryo.

The total fat content of the embryo has diminished considerably; apparently, part of the fatty materials have been consumed in cell metabolism. However, the fat droplets left are found at definite places in all embryos, irrespective of the region of the egg, where the fat had been accumulated during centrifugation: 1°. at the ventral border of the shell gland; 2°. in the stomodaeum at the entrance into the radular sack; 3°. in smaller quantity also in the margin of the mantle fold. Further, in normal embryos of this age, the location of the fat droplets is the same. As a matter of fact, the demonstration of the fat droplets in normal embryos is, as a rule, less easy than in experimental animals; probably, the fatty materials in normal embryos are more finely dispersed, whereas in centrifuged embryos the fat granules have fused to larger droplets and are, therefore, better seen. In many cases, however, an accumulation of small fat granules in the shell gland, the stomodaeum and the mantle fold of normal trochophores could be observed.

Thus, the distribution of the fatty materials in embryos developed from centrifuged eggs at the trochophore stage corresponds to that in normal embryos, irrespective of their abnormal position just after centrifuging and in young cleavage stages. It must be concluded, then, that a regulation process has taken place, as the fatty substances have been transported from their original location to the places where they are found in trochophores. It is highly probable that a transport of these substances through the cell walls must have taken place; perhaps, this interchange of substances occurs in the blastula stage between the central processes of the cells.

With this in mind, it is now possible to get a better understanding of the normal development of eggs centrifuged shortly before cleavage. If, as it appears to be the case, the cell walls form no absolute obstruction for an interchange of substances between the cells of the embryo, the development of these eggs offers no special problems, as compared to the development of eggs centrifuged at an earlier stage. In both cases, we may assume that the factors, which are responsible for the localisation of substances in normal eggs (and which, as we have seen above, are located, probably, in the relatively immovable egg cortex, not displaced by the action of centrifugal force), continue to work in centrifuged eggs till a rather late stage of development, and, in this way, bring back to their normal place the substances displaced during centrifuging.

DISCUSSION

1. When unsegmented eggs of *Limnaea stagnalis* are centrifuged during 5 minutes at a velocity of 3800 revolutions per minute, the injurious effects of centrifuging on development are not very dependent upon the stage of operation. This is in contradiction to the statements of Conklin (1910) and Clement (1938), which were, however, based upon too small a number of experiments. Of course, the conclusions drawn by Conklin from his observations relative to this point have lost their value, too. Conklin explained the increase in the injurious effects of centrifuging as the egg approaches the first cleavage by a) increasing differentiation of the egg, and *b*) decreasing opportunities for readjustment of displaced substances. As, however, such an increase in the injurious effects of centrifuging cannot be demonstrated in our experiments, the latter lend no support to the hypothesis of an increasing differentiation of the oöplasm between the maturation and the first cleavage. Furthermore, our observations on the distribution of fat in embryos from eggs, centrifuged between maturation and first cleavage, seem to show that the formation of the cell walls during cleavage does not interrupt the processes leading to a readjustment of the egg substances.

2. It could be demonstrated that many substances, playing an important part in cell metabolism (enzymes, glutathion, vitamin C), are displaced during centrifuging, and accumulated in special zones of the centrifuged egg. If we assume, that these substances have something to do with the determination of the cells (a hypothesis, which is very probable in the light of the experiments of Ries and Lehmann, referred to above), normal development is dependent upon the readjustment of these substances during further development. Our observations show that, in fact, such a redistribution of substances occurs.

3. The study of whole centrifuged eggs reveals that the stratification of the egg into "gray", "clear" and "yellow substances" does not persist indefinitely, but that the gray and yellow substances mingle with the clear zone, so that the latter has disappeared totally some hours after centrifugation. This

was observed by CONKLIN, too; as a matter of fact, however, in his figures 34–45 this redistribution of substances has not been represented. A sharp separation of the three zones of the egg has been drawn, even in those figures, which represent rotating embryos. It is deplorable that exactly these misleading drawings have found their way into many compendia and hand books. If they were right, they would fully justify the conclusion of CONKLIN that "the differently colored substances of these eggs are not "organforming" . . . .", that "the gray and yellow substances are mere inclusions in the protoplasm and that neither are essential to development". But they are wrong and misleading; CONKLIN himself describes the rearrangement of the gray and yellow materials, leading to the disappearance of the clear zone. And our sections show that this readjustment takes place in a far larger measure still than can be observed in whole living eggs, so that in eggs centrifuged shortly after laying a nearly homogeneous distribution of substances has been attained again before the beginning of cleavage. With this in mind, it is clear that the conclusions of CONKLIN are not justified. If the "gray" and "yellow materials" (i.e. the fat droplets and albumen granules) in centrifuged eggs spread evenly through the egg protoplasm, so that the structure of normal eggs is restored, it is impossible to draw any conclusions about the part they play in development.

How, then, has CONKLIN been mislead to such false statements? Our observations give us a clue to answer this question. CONKLIN only studied living and unsectioned eggs. Now, in such eggs the fat zone, as stated above, is white in reflected light, the albumen zone yellow. So, after the disappearance of the clear zone, the egg consists of a white and a yellow half, differing somewhat in size dependent upon the stage of operation. At further development, this appearance is retained during some days; part of the surface of the embryo is white, suggesting the presence of a large mass of fat at this place. If, however, such an embryo is sectioned, or treated with Sudan III, it becomes evident that the fatty substances have been dispersed largely; no accumulation of fat, or only a small quantity of fat granules, can be demonstrated at the white spot. It is evident, then, that the appearance of the whole egg can give but an imperfect impression of its real composition. It is probable that yellow pigment granules and small fat droplets adhere to the egg cortex in the region of the albumen and fat zone of centrifuged eggs; they stay there, when the redistribution of substances occurs, and imitate in this way a stratification, which has disappeared since some time.

4. Our observations prove the readjustment of the egg substances displaced by centrifuging. It should be clear that in this readjustment two different processes are involved. First, there is the dispersion of the substances accumulated during centrifuging, leading to an equal or nearly equal distribution throughout the egg protoplasm. We have observed this dispersion, studying the development of whole living centrifuged eggs; we have followed it in sections of eggs, fixed at different times after centrifuging; moreover, we have demonstrated it for special substances, detectable by histochemical methods in the egg.

Secondly, however, we have to distinguish another process, that is, in some respect, the contrary of the first-named. If, as was admitted by us, some of the substances displaced by centrifuging have something to do with the determination of the cells, a localisation of these substances in special parts of the embryo will take place in normal development. We must assume, then, that normal development of centrifuged eggs is dependent upon a normal localisation of these substances. Readjustment of the egg materials, therefore, does not only involve their dispersion after centrifuging, but also the localisation of determinative substances, bringing about the "chemo-differentiation" of the egg.

It will remembered that in trochophores, developed from centrifuged eggs, the distribution of fat droplets was found to resemble that in normal trochophores, irrespective of the original position of the fat zone after centrifuging. In this instance, thus, the accumulation of a substance in its normal localisation, after its initial dispersion through the egg, could be clearly demonstrated. It is to be expected that the same will hold for other substances of the egg protoplasm. To prove this, it will be necessary, first, to make an extensive study of the localisation of substances during normal development, as far as this is possible with our present methods. This will be the object of another paper.

Summary

1. Unsegmented eggs of *Limnaea stagnalis* were centrifuged during 5 minutes at a velocity of 3800 revolutions per minute.

2. The injurious effects of centrifugation on development are small, and not very dependent upon the stage of operation. 68% of the centrifuged eggs develop into normal little snails.

3. The rate of stratification and the relative proportions of the zones of the stratified egg vary with the stage of operation; evidently, important changes in the physical and chemical composition of the egg protoplasm occur during the uncleaved stage of the egg.

4. The centrifuged eggs are stratified into four zones. The centripetal zone of the egg consists, mainly, of fat, especially unsaturated glycerides. Its structure varies with the stage of operation. The second zone is composed of hyaloplasm; in most eggs, it contains the egg nucleus or maturation spindle. The hyaloplasm contains glutathion. The third zone is a narrow band of small granules, probably mitochondria; indophenol-blue-oxydase, benzidine-peroxydase and glycogen and, perhaps, vitamin C are accumulated in this zone. The fourth, centrifugal, zone of the egg consists of albumen granules; furthermore, it contains special large granules, destined to transform into vacuoles.

5. At further development a readjustment of the substances displaced by centrifugation takes place. First, the accumulated materials disperse through the egg, leading to an equal distribution of substances throughout the protoplasm. Secondly, a localisation of special substances occurs, bringing about the chemo-differentiation of the egg. This redistribution of substances is not completely obstructed by the formation of the cell walls, but may continue after the beginning of cleavage.

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ON THE NOMENCLATURE OF SOME FOSSIL HIPPOPOTAMI

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In 1804 CUVIER published a note on some fossil remains of hippopotami from Montpellier and the Val d'Arno, among which he distinguished a large and a small form. Only CUVIER's "grand Hippopotame fossile" will be dealt with here. At first CUVIER could not separate it from the recent species (CUVIER, 1804, p. 99).

In 1820 the Muséum d'Histoire Naturelle in Paris received a recent adult hippopotamus skeleton, the first to arrive in Europe, from an animal shot by DELALANDE at the lower Berg river, 40 miles from Cape Town. In the second edition of his "Ossemens fossiles" CUVIER gave a careful description of this skeleton; a comparison with the fossil bones he had received in the meantime gave evidence that these bones were too large to belong to the recent species (CUVIER, 1821, p. 315). It was not until 1824 that CUVIER proposed the scientific name *Hippopotamus major* (CUVIER, 1824, p. 527). Two years earlier, however, the specific name *Hippopotamus antiquus* was given by DESMAREST (1822, p. 388) to the animal originally described by CUVIER as "grand Hippopotame fossile". As DESMAREST's note includes a description and a reference to CUVIER's publication, *Hippopotamus antiquus* Desmarest is the valid name according to the Rules of Zoological Nomenclature. There is some confusion as to the author's name; CUVIER is cited as the author of *Hippopotamus antiquus* by LESSON (1827, p. 342), FISCHER (1829, p. 426), FALCONER and CAUTLEY (1836, p. 51) and FALCONER (1868, p. 140). This species, which is now known to have inhabited Europe in the pleistocene period, S of the line about connecting Yorkshire, Antwerp, Mosbach, Aargau, Pressburg, is so closely related to *Hippopotamus amphibius* L. that many authors do not regard it as a distinct species, e.g., BLAINVILLE (1847, p. 61), LYDEKKER (1885, p. 277), DAWKINS (vide MAJOR, 1885, p. 8), BOULE (1910, p. 193) and REYNOLDS (1922). The latter gives a review of the literature.

The major difference between *antiquus* and *amphibius*, however, is that of the size of the teeth, especially the lower C and I_1, which in the fossil species occasionally reach diameters, larger than ever found in *amphibius*.

There is some uncertainty about the priority of the name *Hippopotamus antiquus* Desm. BLAINVILLE (1847, p. 55 footnote) remarks that FISCHER has used the specific name *maximus* before CUVIER had published the name *major*. In SHERBORN (1928, p. 3925) *Hippopotamus maximus* is mentioned, but the only reference given is BLAINVILLE (1847, p. 55)! According to SHERBORN (l.c., p. 3765) FISCHER is the author of *Hippopotamus macrodon* (FISCHER, G., 1814. Zoognosia tabulis synopticis illustrata, ed. 3, III, p. 331, non vidi), which just as *Hippopotamus magnus* Rafinesque (Specchio d. Sci. e Giorn. Enciclop. di Sicilia II (12), Dec. 1814, p. 183, non vidi) might apply to the *Hippopotamus antiquus* of DESMAREST.

BRONN (1848, p. 589) mentions the name *Hippopotamus major* and gives the following references: "NESTI i Atti Moden. XVIII, 415; – Cuv. oss. I, 304, t. 1, f. 1–5, t. 2, f. 1, 2, 10, t. 4, f. 1–4, t. 5, f. 1–15, 17, t. 6, f. 1–15". NESTI's publication was not available to me, but Prof. G. DAL PIAZ, Turin, kindly informed me that NESTI only used the name Ippopotamo Maggiore, and not *Hippopotamus major*. This is in accordance with a reference to Ippopotamo maggiore by FISCHER (1829, p. 426). Moreover TROUESSART (1898) does not mention NESTI as the author of a scientific name of a hippopotamus. The citations of CUVIER in BRONN do not refer to a scientific name but to the fossil named by CUVIER: "grand Hippopotame fossile".

However this may be, the fact that DESMAREST used the name *Hippopotamus antiquus* in 1822 makes the further use of this name invalid for species of the genus *Hippopotamus* described since 1822.

The name *Hippopotamus antiquus* is mentioned by LESSON (1827, p. 342), FISCHER (1829, p. 426), FALCONER and CAUTLEY (1836, p. 51), FALCONER (1868, p. 140) and WOODWARD (1886, p. 115). It is regarded as a synonym of *H. major* by BLAINVILLE (1847, p. 55) and BRONN (1848, p. 589); we find it in the synonymy of *H. amphibius* in LYDEKKER (1885, p. 277) and in TROUESSART (1898, p. 832; 1905, p. 665).

VON KOENIGSWALD (1934, p. 192, pl. IV fig. 4) proposed the name *Hippopotamus* (*Hexaprotodon*) *antiquus* for a new species occurring with the lower pleistocene Djetis fauna of Java (afterwards also found in the upper pliocene Kali Glagah fauna). From the foregoing it is evident that this specific name in reality is a homonym of *Hippopotamus antiqus* Desmarest, 1822, and as such must be rejected.

As under the present circumstances it is impossible to communicate with Dr. G. H. R. VON KOENIGSWALD to inform him of the present case, and as it is desirable with regard to other researches that VON KOENIGSWALD's species has a valid name, I propose the substitute name *Hippopotamus koenigswaldi* nom. nov. for *Hippopotamus* (*Hexaprotodon*) *antiquus* von Koenigswald, 1934. A complete bibliographical reference to this species is given below.

Hippopotamus koenigswaldi nom. nov.

Hippopotamus (*Hexaprotodon*) *antiquus* von Koenigswald, De Ing. in Ned. Indië, vol. 1, pt. 11, sect. IV, 1934, p. 192, pl. IV fig. 4.

Hippopotamus antiquus von Koenigswald, Proc. Kon. Ak. v. Wet. Amst., vol. XXXVII, 1934, p. 655, fig. 3, 4.

Hippopotamus (*Hexaprotodon*) *antiquus* von Koenigswald, Proc. Kon. Ak. v. Wet. Amst., vol. XXXVIII, 1935, p. 193. (Djetis).

Hippopotamus antiquus von Koenigswald, Id., p. 194 (Kali Glagah).

Hippopotamus (*Hexaprotodon*) *antiquus* von Koenigswald, De Ing. in Ned. Indië, vol. 2, pt. 10, sect. IV, 1935, p. 86, fig. 3, 4.

H[*ippopotamus*] *antiquus* von Koenigswald, Tijdschr. K.N.A.G., ser. 2, vol. LII, 1935, p. 540.

Hippopotamus antiquus von Koenigswald, Quartär, vol. 2, 1939, p. 30 (Kali Glagah).

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ON THE FORMATION OF BANKS BY MYTILUS EDULIS L.

BY

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I. INTRODUCTION

Mytilus edulis L. occurs on the northern hemisphere on the coasts of the Atlantic Ocean, in Europe as well as in America. The mussels are restricted to the littoral zone (White, 1937). In this area they are not regularly distributed, however, but form banks. This investigation is an effort to explain how this formation of banks is brought about. The work was carried out from July till October, 1939, at the Zoological Station of the Netherland Zoological Society, Den Helder. I am greatly indebted to Dr. J. Verwey, Director of the Station, for suggesting the subject to me, for his constructive criticism and help in the preparation of this paper.

II. PRELIMINARY OBSERVATIONS

The Harbour of Den Helder, the Nieuwe Diep, retains its depth by means of a system of basalt dikes, the Leidam and the Vangdam. These dikes enclose muddy sandflats (see fig. 1 of Kuenen's as well as of this paper), the so called Zuidwal, running dry for the greater part at low tide. The Zoological Station have been making thorough ecological investigations in this area during a number of years. To this end the flats have been divided, by means of concrete poles, into squares with sides of 200 m. The poles, standing on the angles of the squares, are drawn up in rows indicated by letters, whereas the poles themselves bear figures.

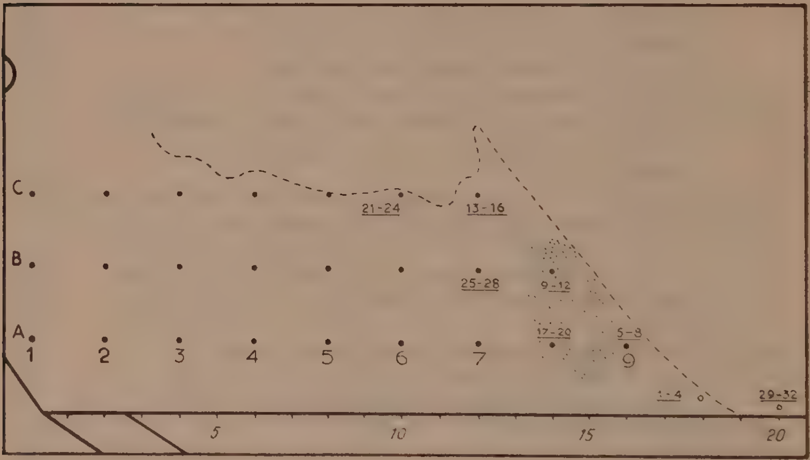

Fig. 1. Map of the Zuidwal Sands, compare also text and fig. 1 and 18 of Kuenen's paper. Italic figures denote hectometer poles on Vangdam, A, B, C the rows of concrete poles, the upright figures the numbers of the latter. Underlined figures give the figures of the tiles laid out. Dotted area represents the bank of young, newly settled mussels.

There have been mussel banks in this area for several years and they have served as material for an investigation into the causes of the distribution of *Mytilus* on these flats by Kuenen. Besides mussels especially the lower eastern part of the flats possesses a rich population of cockles (*Cardium edule* L.). The ecology of this species was studied by Kreger; during his investigation dense patches of these animals were lying chiefly near pole A6 and A7 and between A7, C7, B8, A9 and the

Vangdam. These cockles, which according to KREGER chiefly belonged to the yearclass 1936, died for the greater part as a result of the severe frost of December, 1938. Many of them have been gradually laid bare by the current and the young mussels have attached themselves to them. In the beginning of July, 1939, the length of these young mussels varied from almost 1 to ± 5 mm.

The way in which the mussels are attached to these cockles is remarkable. From the sand upwards they form a girdle wholly or partly enclosing the *Cardium* shells. Sometimes the top of the shell is also covered. By the "top" I do not mean the umbo, but the part of the shell which accidentally projects farthest from the sand. The mussels sit close together without any intermediate space, their ventral side against the outside of the cockle. All umbones point downwards, those of the bottom row of mussels stick into the sand. As far as there is one single mussel on the convex ridged side of the cockle it is placed in a hollow between two ridges and not on the ridge. In this case too the umbo points downwards.

When only one valve of the cockles projects partly from the sand the mussels are much more frequently found on the smooth inside than on the ridged outside. Here too they lie with the ventral side against the cockle. In the median line of the shell the umbones of the mussels point straight downwards, but towards the sides they make continually smaller angles with the horizontal. The longitudinal axes of the mussels may be compared to the slats of an outspread fan. The backside of each mussel protrudes from the cockle shell, so that ex- and inhalent apertures are free.

Many cockles have the two valves wholly or partly opened and are stuck in the sand with the dorsal side upwards. Between the umbones mussels may occur, their ventral side now placed horizontally; consequently, the umbo does not point downwards. We may conclude from the growth of *Enteromorpha* on the cockle shell that the cockle has been lying like this for a long time, so that the position of the mussel cannot be accidental.

The sandtubes of *Lanice conchilega* (Pall.), great numbers of which occur among the dead cockles, also bear young mussels. When for the sake of surveyability we restrict our attention to those tubes to which only a few mussels are attached we find their ventral side invariably pressed against the sandtubes. It is on this side that the byssus protrudes from the foot. The young mussels which could not reach the sand stick between the others and their umbones point downwards as well.

Mussels can be found in the same attitude in the grooves between the basalt blocks of the Vangdam or among the numerous specimens of *Balanus balanoides* (L.), or in its shell when the inhabitant has disappeared. Where the young mussels cover the substratum as a serried layer the umbo rarely points straight downwards.

From one of the dolphins in the harbour a twisted steel cable hangs down into the water. The dense cluster of young mussels which have settled down on this cable shows a spiral twist. Apart from this cluster some mussels are scattered over the cable; without any exception they sit in the groove which is formed by the smaller component cables.

The dolphin itself shows from the high water mark downwards a zonal growth of *Enteromorpha*, *Porphyra* and *Balanus*, the latter for the greater part dead. All mussels occurring on *Balanus* sit with the umbones downwards, the ventral sides parallel to the dolphin. Lower down the layer of mussels becomes more irregular and there are many bigger animals which do not exclusively have the umbo pointing downwards. On the wood itself are no mussels, but they do occur in the cracks, where they sit with the umbo perpendicular to the direction of the groove, on the inside.

It appears from these observations that the young mussels have a marked tendency to settle in such a way that they fit into a groove or hollow. When this runs horizontally the mussel lies horizontally, when it runs in another direction the mussel preferably sits in such a way that the umbo points downwards and the exhalent aperture upwards. When the mussels have settled on shells lying on the bottom they sit either between the umbones or between the ridges or on the inner side of the shell, and in these last two cases again preferably in such a way that the umbo sticks into the bottom.

What the mussels obviously want is to settle in such a way as to come in touch with their substratum over a surface which is as large as possible. When the umbo sticks into or between some object or other the surface of contact is enlarged, whereas the intake of water is not hampered, which certainly would be the case if the siphon side were pressed between any objects. There is no doubt that in the way described above the mussels attach themselves firmest and at the same time supply themselves best with water.

As far as I have been able to ascertain SCHWARZ is the only one who describes the attitude of settled mussels. He points out that mussels are mostly found with the umbo downwards and the lower side of the shell upwards. On the perpendicular walls of a mud barge he found them in this normal attitude; against the broad lower side of the ship, however, the mussels sit with the umbo horizontally.

III. EXPERIMENTS ON THE SANDS

It is well known that mussels need a hard substratum in order to be able to attach themselves. More or less detailed observations on this subject are given by SCOTT (1896), HOEK (1909), DELSMAN (1910), FIELD (1916 and 1922) and NELSON (1928). It is very plausible that the continually shifting sand gives no hold to the animals and that this is the reason why mussels occurring on sandy or muddy ground depend for their settling on shells, stones or other hard objects. These objects might serve as a basis for the formation of mussel banks. The wiry tubes of *Lanice conchilega* might benefit the formation of mussel banks as well.

In order to get more certainty, however, about the suitability of a special subsoil as a substratum for mussels and about the possible importance of the pointing downwards of the umbo a small number of simple experiments were carried out: young mussels on the sands were presented with various objects for attachment, and mussels were placed with the umbo pointing upwards instead of downwards.

1. Mussels on shells, eternite and tiles

On a stretch of sand free from algal growth over an area of 16 m² cockle doublets were put into the sand at distances of 50 cm in such a way that the convex side was uppermost. In between 500 mussels, varying from 2 to 10 cm, were sown out as regularly as possible. When the tide rose nearly all the mussels were swept away. After inspection during the next low water it appeared that more than half the number of cockle shells had disappeared or been buried under the sand and upset. In the aggregate 3 mussels were found back on top of the cockle shells between the umbones, and 22 were found each on the inside of the umbo of a cockle, it being impossible to ascertain a preference for the direction of the umbo. About 50 mussels sat in small groups on *Lanice* tubes which I had overlooked when choosing the area. For the rest no mussel could be found outside this plot of ground, which I had marked with corner stones. It was obviously only in the umbones of the cockle shells that the mussels could sufficiently protect themselves against the current, while the tubes of *Lanice* also offered a good hold.

Three following experiments, here given together, led to the same result. Instead of recumbent cockle shells, doublets, standing upright, with the gaping side turned to various directions, were put into the sand up to the hinge in 6 rows of 15 each, at a mutual distance of 20 cm. From the 300 mussels set out 23 were found back, 6 on the outside of the cockle shells and 15 within the shells, all in the umbones.

As an affirmation of KUENEN's observation it also appeared that the surface of an eternite plate was not sufficient for the young mussels to fasten themselves, in this case it made little difference whether the eternite plate was lying on the sand, or was raised on short pegs 10 cm above the ground in order to prevent the little snail *Peringia ulvae* (Pennant) from crawling upon the plate in great numbers.

To collect data about the distribution of the numbers of mussels falling on various parts of the sands groups of tiles were set out. The data about the "spatfall" on these tiles will be discussed further on, but the observations on the attitude of the mussels on the tiles are given here. On the smooth surface of the tiles just a few scattered mussels occurred. Most of them, however, were sitting on the borderline of sand and tile, and many in the grooves. All had their umbones pointing downwards: only in some corners of the grooves the umbo pointed in another direction and the same held good for the small mussels filling the cracks and for those in the trade marks; these animals were mostly 1–2 mm only. The tiles had been put out upright with their broad surfaces perpendicular to the direction of the current (see fig. 2) and the animals could be found on the outside of the tiles exposed to the current as well as protected from it on the lee side.

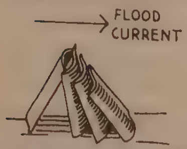

Fig. 2. Tiles set out for spatfall.

2. Experiments with mussels with the umbo upwards

The inducement to these experiments was the discovery that mussels sitting on cockle shells, when they were put down with the umbo upwards, turned round so that they were again sitting with the umbo in the sand. As the animals might have been troubled by sand or mud in their inhalent apertures and turned round in consequence I tied cockle shells with mussels on them to horizontal laths, which had been fastened to poles about 10 cm above the sand. At low tide these laths did not fall dry. When tying up the cockle shells I took care that the rope did not come within 1 cm from the mussel, so that the animal could not attach itself to it without moving; a possible move of the mussel towards the rope could then easily be noticed.

I expected that the result would be dependent on the direction of the lath with regard to the direction of the current and I therefore placed two laths perpendicular to each other. Moreover, front- and backsides of the laths, in relation to the current direction, were indicated by A1, A2, B1 and B2 respectively (see fig. 3). For the rest I did not only use cockles, but mussel shells as well, and I discerned between mussels sitting together in groups of 2 or 3 and such that were sitting singly on the shells, because the latter might sooner show an inclination to move than those sitting firmly attached in a group.

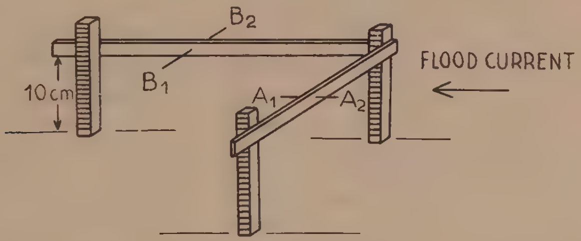

Fig. 3. Laths to which mussel and cockle shells, with mussels attached to them, were tied. For further description see text.

The position of the animals was examined after each high tide. For each series new test animals were used. The protocols have been deposited with the Zoological Station. A short survey is inserted at the end of this paper. The results follow below; they are given in percentages.

Tied up to		on cockles	on mussels	average
A 1	disappeared	34	45	39,5
	same attitude	26	20	23
	moved, umbo turned round	37	30	33,5
	moved, umbo not turned round	2	4	3
A 2	disappeared	27	45	36
	same attitude	40	10,5	25,5
	moved, umbo turned round	26	37	31,5
	moved, umbo not turned round	5,5	5	5,3
B 1	disappeared	28	53	40,5
	same attitude	36	18	27
	moved, umbo turned round	27	18	22,5
	moved, umbo not turned round	6	8	7
B 2	disappeared	42	48	45
	same attitude	29	13	21
	moved, umbo turned round	20	14	17
	moved, umbo not turned round	6	20	13

	average of A 1 and A 2	B 2 and B 2	A 1, A 2, B 1, B 2
disappeared	38	42.75	40
same attitude	24	24	24
moved, umbo turned round	32.5	19.75	26
moved, umbo not turned round	4	10	7

These experiments with mussels which have the umbo turned upwards show the following:

1. When mussels are placed in the current with the umbo upwards at some height above the bottom, so that they cannot be directly troubled by bottom material (mud, sand), the number of mussels seeking another place to settle is extra-

ordinarily great. For in the experiments described above these are all the animals which did not keep the same position, in the aggregate upwards of 75 per cent. A great part (40%) of these disappear, possibly by being carried away by the current. The rest was found back on the inside of the shells, between shell and lath, between two shells lying closely together, between the ropes with which the shells had been tied, etc., consequently in all places where two planes make an angle.

2. The mussels which move to another place have a marked tendency to settle in such a way that the umbo points downwards. This inclination seems strongest with the mussels of the A-lath, which stands perpendicular to the current. Here an average of 32,5% has the umbo downwards and 4% the umbo upwards, so that the relation is 8 : 1. The inclination to settle with the umbo downwards is least pronounced with the animals of the B-lath, which had been put up parallel to the direction of the current. Here an average of 20% has the umbo pointing downwards and 10% upwards, so that the relation is 2 : 1.

3. It seems to make no difference to the mussels whether they have been placed on the side of the A-lath facing the flood, or on that facing the ebb current. The number of experiments is too small, however, to decide on this point.

4. It makes a difference whether the mussels in the current sit on a ridged cockle or on a smooth mussel shell. An average of 48% of the mussels disappears from the mussel shells, of 33% from the cockles. This experiment is an affirmation of all those data which indicate that a smooth surface gives but little support to the animals.

5. An average of 24% of all mussels, though sitting with the umbo upwards, does not change place or attitude at all. These 24% contain mussels in groups as well as solitary ones, so that their clinging to the original attitude is not because they are kept in their places by the byssus threads of their neighbours. For figures see the tables at the end.

It is a pity that, when carrying out these experiments, I did not sufficiently realize that I should have set out mussels with the umbo downwards as well as upwards. For we are faced by two possibilities: 1. the change of place, 2. the change of attitude. When the animal changes its place the reason may be that the umbo was pointing upwards, but it may also be that the place was unsuitable. When the animal only changes its attitude it is certain that it was not troubled by the wrong place, but by the wrong attitude. Every change of attitude, however, is properly speaking, accompanied by a change of place and I therefore did not differentiate these two. Consequently, it cannot be ascertained in which part of the cases the wrong attitude and to what degree the wrong place was decisive. As stated above the question might have been solved by setting out the mussels both with the umbo downwards and upwards.

As to the preference of the mussels to settle with the umbo downwards, however, there is no doubt.

Conclusions concerning the experiments in the field

It appears from these experiments that the mussels do not settle on a sandy bottom, nor on smooth surfaces. On a rough surface they settle if it is sloping, preferably in such a way that the umbo points downwards, but this is not necessary.

A first requirement is probably a hard surface of a certain size. A grain of sand is too small, on the other hand a small stone or a shell will already satisfy a young mussel. KUENEN's experiments (1941) make it probable that the current has some influence in this respect, as they show that the mussels do not fix themselves when the substratum may be set in movement, as is the case with loose sand.

The surface in question may not be smooth. The disappearance of mussels from a smooth surface does not prove that they cannot settle on such a surface, it is also possible that the latter does not meet their thigmotactical needs. The animals preferably settle in such a way that they are on both sides enclosed by the substratum, so that they are caught between two planes forming an angle with each other.

It follows from the experiments that it is not necessary for the mussels on a sloping surface to point the umbo downwards. All the same, the greater part of them take care to do so, also when there is nothing of a disturbing influence of sand. But if the mussels after attachment are put with the umbo upwards a certain number (in the experiments 24%) do not change their attitude. Quite probably this reaction is influenced by the current, see number 2 of the above conclusions.

It would be interesting to investigate whether the gravitation is the directing factor in this settling and in how far the reaction can be stimulated or at least influenced by other factors.

It should finally be pointed out that, properly speaking, neither the observations nor the experiments conclusively show whether the mussel tries to bring merely its umbo or also its whole ventral side into the closest possible contact with the substratum. It would certainly be worth while to solve this question experimentally.

IV. SETTLING OF MUSSELS ON THE SANDS

The preceding experiments show that mussels need a hard and rough subsoil in order to maintain themselves. It has not yet been made clear, however, why banks are formed by the mussels after they have settled.

Two questions immediately suggest themselves:

1. Is the formation of banks the result of a favourable combination of external factors (substratum, temperature, salinity, strength of the current, and – connected with the latter – food supply), such as is only found in a few places, and do the animals accumulate in these places because the larvae carried along by the currents find favourable conditions there and consequently settle down?
2. Or do the mussels seek each other actively and independent from the factors mentioned, as a result of something like a social instinct? If so, how do they find each other?

To obtain indications as to this matter I tried to examine the distribution of spatfall on the flats by means of tiles, which had been set out to that end. In principle the method used was that practised in Zeeland to catch oyster larvae (Havinga, 1932). Clean tiles were put out in groups on the sands, three at a time against each other, supported by a fourth under a sharp angle. The position of the tiles was such that the broad surface stood perpendicular to the direction of the current (see fig. 2).

It was possible for the unaided eye to discern the recently attached mussels on the tiles as somewhat yellowish spots. At first their identification was made a bit difficult by the fact that *Balanus*, which also settled on the tiles, resembled them, but soon it was possible to distinguish these from the young mussels, without a lens too, by their difference in colour and attitude.

According to Delsman (1910) the larvae on the point of attaching themselves are about 0,25 mm large. The smallest attached mussel he found measured 0,28 mm. According to

HAVINGA (1932) the recently attached mussels are 0,25–0,30 mm.

The first group of tiles (1–4, compare fig. 1) was set out on the 14th of July on the sands near hectometerpole 18 at the border of an old mussel bank. The second group (5–8) was put out near pole A9 and the third (9–12) near B8. After 4 high tides the mussels on the tiles were counted, the tiles themselves cleaned and set out once more.

Date	Group	Number of tile	Number of mussels	Totals	Remarks
July 16th	1800 m	4	4	28	sandy, near old mussel bank
		3	4		
		2	4		
		1	16		
	A 9	8	4	41	sandy, many tubes of *Lanice* and cockle shells with *Enteromorpha* growth
		7	21		
		6	9		
		5	7		
	B 8	12	± 100	± 250	same conditions as near A 9
		11	± 50		
		10	20		
		9	± 80		

On the 18th of July the tiles were again inspected after 4 high tides.

Date	Group	Number of tile	Number of mussels	Totals	Remarks
July 18th	1800 m	4	2	17	
		3	4		
		2	3		
		1	8		
	A 9	8	44	222	
		7	85		
		6	22		
		5	51		
	B 8	12	27	352	
		11	98		
		10	123		
		9	104		

Most of the animals on the tiles were from 0,5 to ± 1 mm long, unpigmented or with a dark margin; some were quite dark already.

After this the tiles up to and including number 28 were set out and also inspected after 4 high tides.

Date	Group	Number of tile	Number of mussels	Totals	Remarks
July 22nd		4	12		
		3	16		
	1800 m	2	10	56	
		1	18		
		8	6		
		7	7		
	A 9	6	13	56	
		5	26		
		20	65		many *Enteromorpha* and *Lanice* tubes; one mussel of 5 cm.
		19	75		
	A 8	18	±150	±590	
		17	±300		
	B 8	12	31		
		11	66		
		10	47	222	
		9	78		
		28	15		
		27	5		
	B 7	26	4	32	
		25	8		
		16	37		
		15	29		
	C 7	14	21	197	
		13	110		
		24	31		
		23	18		
	C 6	22	18	68	
		21	1		

The occurrence of these strikingly great numbers of young mussels near A 8 and C 7 was caused by the fact that tubes of *Lanice* had grown up against the tiles and that the mussels had formed regular clusters against them. The great number of mussels on the tiles near B 8 could not be explained in this way, however.

After once more 4 high tides the tiles were inspected on the 26th of July.

Date	Group	Number of tile	Number of mussels	Totals	Remarks
July 26th	1800 m	4	25	69	many specimens of some mm only
		3	15		
		2	16		
		1	13		
	A 9	8	85	243	many specimens of some mm only
		7	75		
		6	83		
		5	under the sand		
	A 8	20	42	137	many specimens of some mm only
		19	50		
		18	32		
		17	13		
	B 8	12	92	443	high figures are due to the presence of *Lanice*
		11	130		
		10	97		
		9	124		
	B 7	28	39	246	0,5 mm and smaller
		27	98		
		26	37		
		25	72		
	C 7	24	71	205	0,5 mm and smaller
		23	63		
		22	33		
		21	38		
	C 6	16	100	188	0,5 mm and smaller
		15	88		
		14	under the sand		
		13	the sand		

After this it was not before the 7th of August that I was able to clean the tiles again and set them out. After 4 high tides they were inspected.

Date	Group	Number of tile	Number of mussels	Totals	Remarks
Aug. 9th	2000 m	32	3	15	most mussels some mm long
		31	1		
		30	6		
		29	5		
	1800 m	4	0	7	most mussels some mm long
		3	6		
		2	0		
		1	1		
	A 9	8	6	21	most mussels some mm long
		7	5		
		6	2		
		5	8		
	A 8	20	12	37	most mussels some mm long
		19	18		
		18	7		
		17	0		
	B 8	12	11	54	largest mussels reaching ± 10 mm
		11	30		
		10	8		
		9	5		
	B 7	28	3	5	largest ± 5 mm
		27	1		
		26	1		
		25	0		
	C 7	16	3	6	1 mm and smaller
		15	2		
		14	0		
		13	1		

The object of these experiments, namely to get an insight into the relation between spatfall and formation of banks, has not been attained. For a proper spatfall it was obviously too late. Only once did I succeed in finding larvae of a Lamellibranchiate in the plankton samples from the sands and from the Nieuwe Diep. These were, moreover, quite probably no mussel larvae, because the characters used for identification by Delsman (1910), Hoek (1909), Kaendler (1927) and Stafford (1906–1910) were missing.

The 26th of July was the only time that I found many very small mussels, not longer than 0,5 mm, near C 6, C 7 and C 8. They were yellowish and transparent, with a purple margin. Some were somewhat younger still and lacked this margin. It is possible, however, that even here we were not concerned with proper spatfall, but with young animals which came from deeper water, see below.

The question arises where these young animals come from. When even a group of 4 tiles during 4 tides catches some hundreds of mussels then enormous numbers of metamorphosed young mussels must be present on or above the sands. It must have been impossible for these animals to reach the tiles by crawling, as experiments in a basin with running water showed that young mussels need 2–3 hours to crawl 10 cm, while they get stuck in the end. Near C 6 the tiles stood at a distance of more than 200 m from the nearest banks of young mussels and the crawling mussels would, moreover, not have found any hold on the loose sand in the strong current during ebb and flood. So it is most plausible to assume that the mussels were carried along by the current. Now KUENEN has shown that marked mussels set out on the Zuidwal were all removed in the direction of the flood current which has a greater maximum strength than the ebb. Consequently, we may perhaps assume that here too it is chiefly the flood which carries the animals along. The fact that the mussels nearer the dike were larger than those farther removed from it (see the tables above) might, moreover, be an argument in favour of this assumption. For a possible explanation for their increase in size would be that the young mussels which are transported by the current from places outside the sands settle when conditions to this end are favourable, detach themselves after some time, because conditions for the larger animals are no longer so favourable, are again carried some distance, attach themselves once more, etc., in the course of which process they increase in size. So we should have to assume that somewhere outside the sands great numbers of very young mussels get detached, to be carried by the current to other places. In this connection the occurrence of very young mussels in countless numbers on the cauloid of *Fucus vesiculosus*, occasionally on *Enteromorpha* spec., very often on *Chondrus crispus* and *Polysiphonia* spec. (see also DELSMAN, 1910, fig. 3) – HOEK (1909) also mentions Hydroid colonies in this connection – is striking, whereas we never find somewhat older mussels, nor young ones of a length of half a cm on these algae, not even in fairly quiet water. So they must have disappeared from them very soon after their metamorphosis (shortly after the first spatfall) and the supposition that the mussels after originally having attached themselves to the algae detach themselves after some time of their own accord in order to be carried along by the current again – this time as a little shell – is very obvious.

WILSON (1937) has pointed to the ability of some worm species to lengthen the duration of their larval life when they cannot find a good substratum. Their larvae live longer in clean glasses than in aquaria with a gravel bottom. He also points out that the mollusc larvae studied by miss LEBOUR (for literature see WILSON) are able to crawl as well as to swim for a short period at the time of metamorphosis from larva to definite form. Further COLE and KNIGHT JONES (1939) with regard to oyster larvae state that the period these animals can crawl as well as swim may last for some days if they do not find a suitable place for settling. Consequently, the animals to some extent have the possibility of moving when they are unable to find a good substratum during the dangerous period of settling.

Young mussels, however, are good crawlers for a long time after their metamorphosis, while they obviously to a great extent use the current for their transport. In this connection the observation of NELSON (1928) – although it has never been affirmed – is important. According to it the ability of the dissoconch stage of *Mytilus* to float is enlarged by the secreting of a bubble of gas in the hindmost part of the mantle cavity, so that the animals can be transported over great distances in spite of the reduction of their velum. They are drifting with the umbo downwards and as soon as the dissoconch touches some object the foot is protruded, while mantle and valves are kept open, so that the gas bubble may escape. This might explain the ease of transport over considerable distances. In our case, however, we have to do with much larger animals. At the end of this paper I will return to this question.

V. LABORATORY EXPERIMENTS

Whereas from the observations and experiments described the spatfall proper has not become known the observations on the tiles indicate that young metamorphosed mussels occur in the water scattered over the whole of the sands and settle everywhere if only a suitable substratum can be found.

Yet the old mussels live on the sands almost exclusively in more or less large banks and the question remains how the formation of these banks takes place. HOEK (1909, p. 181) is not inclined to assume that the floating brood are able to perceive sensorily which places of the bottom are suitable for their development, but it seems no more probable to him that the mussels sink to the bottom over the whole surface, only to survive where conditions are favourable. HOEK concludes from the dense population of the so called mussel seed banks that the young mussels fall down in great quantities in given places, because there the external conditions are favourable for spatfall. According to HOEK the formation of a mussel bank would thus be a passive process, as he cannot believe that the mobility of the young mussels, which is actually present, enables them to cover great distances.

From the literature mentioned above and from my own experiments the impression is gained, however, that, properly speaking, the young mussels fall down everywhere and after that move along great distances all the same, actively or not. Now, if, besides the mobility of the earliest stages, the current is brought to the fore as an important factor in the formation of a mussel bank, it is still difficult to understand how the scattered mussel population concentrates in the end into only a few banks. The supposition that there is still another factor which brings the mussels together, namely the ability of the animals to perceive each other in one way or other, seems justified.

In order to obtain certainty in this question experiments were necessary. They were made in the laboratory, as we can so much better control the different factors here than in the field; they aimed at settling the question in how far young mussels set out amongst congeners find these, and if they do find them how they succeed in this.

The experiments were carried out in concrete asbestos aquaria of 100 × 60 × 50 cm, which had served for a long time as such and of which might thus be assumed that they would not give off harmful components to the water. In these containers the young mussels were set out in shallow water amongst congeners which had been glued to the bottom to prevent them from moving. By gluing these animals on in equidistant rows at equal distances from each other and placing the test animals in between, the distance of each test mussel to its 4 glued on neighbours was equally great. In order to investigate which characteristics were decisive for the test mussels in the possible search for or attaching near congeners the glued on living mussels were presented over against empty shells, or mussels with byssus were presented over against mussels without, solitary mussels over against groups, or mussels were presented opposed to pebbles and single pebbles opposed to groups of stones, or groups of stones with mussel odour opposed to groups without such odour, etc.

The gluing on of the mussels took place by means of a viscous solution of celluloid in acetone; to that end they were first dried and the smooth periostracum was rubbed off. Dead and living mussels were glued on in the same way, with one valve on the bottom; the living mussels were then all the same able to open their shells and keep water circulating during the experiments. In order to make the glue stick I let the shells dry half an hour or longer, a performance the mussels can stand without any difficulty. In doing this the acetone evaporates for the greater part, but it cannot be avoided that it partly dissolves in the water and may give off some taste or smell. Yet this cannot much influence the choice, as all objects were glued on in the same way and consequently all must have given off the same taste or smell.

The "dead mussels" were empty shells of scalded mussels; after removal of the flesh the shells were 10 times rinsed with alcohol 96%.

For each test series I let the used sea water run away, and refilled the container with water rich in oxygen to a height of some cm. Most experiments were carried out in stagnant water; in the case of living mussels which were not allowed to leave their places the water was more frequently refreshed before the experiment was started. Once every two days each container was thoroughly cleansed with alcohol 96% in order to prevent possible mistakes on account of taste or smell of the glued on objects; for they might have retained a smell of the mussels which had settled on them during previous experiments. Later on I went as far as to remove the living glued on mussels after each experiment and to rinse the basin with 80% alcohol. After this the alcohol – now diluted by sea water – was siphoned away and replaced by alcohol 96%, which was changed 2 or 3 times. The new mussels were not glued on before the container was thoroughly dry. After the celluloid glue had hardened the basin was again once or twice rinsed with sea water.

In order to rule out a possible hampering or otherwise disturbing influence of the daylight the experiments were carried out in a dark room.

WILSON (1887) discovered that the larvae in the stage with four gills have an eye spot on both sides at the base of the first inner gill arch. According to PELSENEER (1899) these eyes still exist with full grown mussels. They are fairly well developed, but we may doubt their value, because the eye spots get further away from the opened posterior margin of the valves during growth; the light penetrating to the eyes will therefore be very weak.

Besides these eyes the mussel in its mantle margin has a light brown pigmented organ, which is susceptible to light, while the foot has dark brown pigment and is sensitive to light as well (WHITE, 1937).

As a rule the experiments lasted 9 hours, during which the mussels made their choice; after this the position of the animals was checked. A few times I examined their position once more 24 hours later and in the 10 cases examined, referring to a total of some hundreds of mussels, it occurred twice that a mussel, not yet having found a fixed point for attachment, had crawled on. One formed part of a series of 36, the other of one of 55. From experiments made by daylight it, moreover, appeared that young mussels under favourable conditions had found a place for attachment after 2 hours and did not change place after this, at least not in stagnant water. In running water it occurred in 10–12% of the cases that solitary mussels still changed their place after one day, but this does not lead to a wrong result in the case of these experiments either, see below (p. 321).

I took care not to include in my counts any mussels which might attach themselves to a living or dead mussel or a stone after another had previously reached the same spot. For if a mussel settles on a dead one (or a stone) after another had arrived there before the final result does not show whether it was the dead or the living mussel which caused number 2 to attach itself. For the same reason mussels sitting on an „indifferent'' mussel were not counted. An "indifferent'' mussel is a mussel which has not joined another and has got stuck on the way by some reason or other.

When we try to make out which characteristics might be decisive for the mussels to attach themselves to congeners the supposition seems obvious that the animals perceive each other chemically and the first aim of these experiments therefore was to demonstrate the part this chemoperception might play. During the experiments, however, it soon became apparent that in "catching'' the young mussels the size of the circumference of a mussel group is obviously of some importance. Because of this importance the experiments are given here in another order than in which they were really made.

1. Living solitary mussel over against mussel group in stagnant water

If we assumed that the mussels let themselves transport by the current as long as this is necessary for meeting congeners we might imagine that a solitary mussel has less chance of being found than a group of mussels and the latter again much less than a genuine mussel bank. When therefore we should find a positive relation between the size of a mussel group and the number of mussels it "catches'' this might point to the possibility that mussels reach their congeners in a completely passive way. It must immediately be added that even in this case it is quite possible that, besides, the animals possess means to "identify'' each other.

In a stone container 5 rows of solitary mussels alternating with mussel groups, totalling 40 of each, were glued on with celluloid glue. Their mutual distance was about 7 cm. Between them 60 free mussels were set out. The groups were pieces torn off a colony, the animals were of the yearclass 1939 and 2,5 cm long at the utmost. The torn off pieces had been chosen as much as possible of one and the same size. At first they lay spread out flatly on the bottom, but after one night already they grew higher of their own accord and their base became smaller, because the mussels joined each other closer, mutually binding themselves with new byssus threads; after the second night the colonies were even more globular. The average circumference of the solitary glued on mussels was 4 cm, that of the groups

9 cm. I took the sum of all circumferences divided by the number of individuals or groups respectively as average circumference. The circumference was measured by putting a thin rope round the base. The free mussels were not removed. Yet the increase in size of the groups was negligible, as these mussels filled the holes between the others. The test mussels had been made recognizable by scraping off the periostracum of both valves, so that they looked bright blue in the water.

Series	Number of test mussels	Group		Solitary		Indifferent	
		alone	arrived later	alone	arrived later	alone	arrived later
1	60	42	–	8	–	10	–
2	60	32	–	18	–	10	–
3	60	35	–	15	–	10	–
4	60	29	–	14	1	17	–
5	60	30	–	11	–	19	–
6	60	35	–	9	1	15	–
7	60	26	–	11	1	22	–
totals	420	229 (54%)		86 (20%)		103 (24%)	

The number of mussels reaching a group is very great, 54%; the number of those attaching themselves to a solitary mussel is 20%. The relation between these two is 2,7 : 1. About the same relation (2,2) is found between the circumferences of group and solitary mussel, so that the experiment may point to the evidence that the number of mussels reaching a group or a solitary mussel is dependent on the circumference.

2. Living mussel over against group of stones

It appears from the preceding experiment that a group of mussels "attracts" more animals than a solitary individual. This may be caused by the stronger smell of the group as opposed to the individual. It may also be, however, that a group, because of its so much larger surface, has a greater chance of being met. If now the group of mussels is replaced by a group of stones the relation between the circumferences of solitary mussel and group of stones may no longer be decisive in case the smell really has any influence.

Groups of stones and single mussels, alternating with each other, altogether 25 of each, were glued on in 5 rows of 10. Each group consisted of 5 stones, placed in the shape of a star. The average circumference of a group measured 13, that of a solitary mussel 4 cm. Between them 36 free mussels were set out.

Series	Number of test mussels	Group of stones		Solitary mussel		Indifferent	
		alone	arrived later	alone	arrived later	alone	arrived later
1	36	16	1	9	–	10	–
2	36	14	–	5	–	17	–
3	36	19	–	7	2	8	–
4	36	20	2	4	2	8	–
5	36	27	1	4	–	8	–
6	36	16	–	3	–	17	–
totals	216	112 (52%)		32 (15%)		68 (31%)	

The number of mussels on a group of stones is 3,5 times as large as that on a solitary mussel; about the same relation exists between the circumferences of the group of stones and the mussel. So this experiment obviously points to the size of the circumference being of greater importance than the smell.

3. Small stone over against group of stones

The preceding series of experiments prove that the test mussels also content themselves with stones instead of congeners and that the numbers attaching themselves to the groups of stones and the single mussels bear the same relation as their circumferences. The experiment is not exact, however, as mussel individuals have been compared here to groups of stones. Parallel to experiment 1 therefore small stones and groups of them were also compared with each other. 25 single stones and the same amount of groups were put in 5 rows of 10, each group consisting of 5 stones glued on in the shape of a star. The average circumference of a single stone was 5, that of a group 13 cm. Between the stones 36 mussels were set out. For the sake of completeness it must be remarked that I washed the basin with alcohol after each experiment in the way described above.

Series	Number of test mussels	Group of stones		Single stone		Indifferent	
		alone	arrived later	alone	arrived later	alone	arrived later
1	36	22	1	2	–	11	–
2	36	21	1	2	–	12	–
3	36	21	2	–	–	12	1
4	36	22	1	4	–	9	–
totals	144	86 (60%)		8 (5,5%)		44 (30%)	

A group of stones appears to attract a great deal more mussels than corresponds with the relation of the circumferences. The number of mussels having arrived at a single stone is so strikingly small that we must perhaps seek the reason in the bad hold a small and smooth stone offers to a wandering mussel. Probably the mussels actually did find the single stones, but often left them again. In any case the experiment points to the fact that it need not necessarily be the taste or smell, which makes the group of mussels attract more congeners than the solitary individual.

4. Large stone over against group of stones

A possibility which might explain the unexpected results of the foregoing experiment is perhaps that a single stone does not sufficiently satisfy the thigmotactical needs of a mussel and is consequently at a disadvantage as opposed to a group with sharp angles between the component parts. In experiments made by daylight I had namely two or three times seen mussels which had reached a glued on congener leave it again after some time. As we know from the preliminary observations and from the small experiments made in the field that not every object is suitable for attachment it might be that a single stone does not sufficiently meet the mussel's wants.

I therefore repeated the previous experiments in such a manner as to replace the single stones by others presenting in my opinion enough support to the mussels to attach themselves. They were large and angular, and in order to exclude a possible unfavourable influence through the difference in size I chose them as much as possible of the same dimension as the groups. The average circumference of a group measured 14,6 cm and that of a single stone 11,3 cm; consequently, the average relation between the circumferences of a group and a stone was 1,3 : 1.

Each time after two experiments the basin was cleaned, and the places where a mussel had been sitting were carefully scraped off in order to remove possible byssus threads. Further explanation of the measure will follow in experiment 9, foot note. 30 single stones and 30 groups, each consisting of 4 stones in the shape of a star, were glued on in 4 rows of 15 between which 42 mussels were set out.

Series	Number of test mussels	Group of stones		Single stone		Indifferent	
		alone	arrived later	alone	arrived later	alone	arrived later
1	42	17	–	12	–	13	–
2	42	12	–	18	–	12	–
3	42	21	1	11	–	9	–
4	42	17	3	11	–	11	–
5	42	10	–	15	3	12	2
6	42	20	–	12	1	9	–
7	42	14	–	14	–	14	–
8	42	18	1	14	–	9	–
9	42	8	–	13	–	21	–
totals	378	137 (36%)		120 (31,7%)		110 (30%)	

The relation between the numbers of mussels on a group of stones and a single stone is 1,1 : 1, thus corresponding very well to the relation in size between group and single stone, which was 1,3 : 1. So a large stone attracts – if only it offers sufficient hold – as many mussels as a group of the same size. The circumference alone may therefore very well be the cause of a group of mussels attracting more young congeners than a solitary animal.

5. Living over against dead mussel in running water

The foregoing experiments give the impression that there is a relation between the size of an object and the number of mussels it attracts; the larger the object the greater the number of mussels settling on it.

Opposed to this, however, it remains possible that the living mussels give off a smell which may attract congeners, and it was therefore self-evident to carry out an experiment in which young mussels were given the choice between living and dead ones.

In a stone basin living and dead mussels, 57 of each, were alternately glued on with celluloid glue in 6 rows of 19; small ones from 8 mm upwards and large ones up to 3 cm were used in a heap. The intervening space between 4 glued on mussels was a square with sides of about 6 cm; in the aggregate there were thus 5 × 18 = 90 squares, but only the middle stretch, consisting of 3 rows of squares, thus containing 54 of them, was used. This measure served to prevent the mussels near the outer row from crawling out of the field too soon. It appeared to be an unnecessary precaution, however, and hence was given up later on.

In the first series only 1 mussel was set out in the centre of every square, whereas 2 were set out in the following series. In the 3rd series 5 mussels got lost.

As this experiment was in reality the first I made and as I wanted to imitate to a certain extent the conditions on the sands the basin was fitted up for running water. The water entered it by three tubes, which had been fixed at some distance from each other to one of the short sides. By means of this installation I hoped to achieve that the strength of the current would be equally great all over the basin, but I did not succeed here, for along one of the sides a counter-current developed and a number of whirlpools were spread over the whole of the water. Near the tubes free mussels attached to the glued on mussels in rare instances only. The current was too strong here, so that the mussels were dragged to areas where their protruded foot could better succeed in finding a hold. At some distance from the opening of the tubes the groups of attached mussels became therefore larger. Because of the disadvantages connected with working in running water I always experimented with stagnant water later on.

Series	Number of test mussels	Living mussel		Dead mussel		Indifferent	
		alone	arrived later	alone	arrived later	alone	arrived later
1	54	11	3	8	–	32	–
2	102	22	4	20	8	40	8
3	102	20	10	13	10	34	10
4	102	32	23	14	6	27	–
totals	360	85 (23,6%)		55 (15%)		133 (37%)	

This experiment shows that mussels searching for a hold show a preference for living mussels to dead ones. The number of indifferent animals, which do not join another mussel, is very great however.

6. Living mussel over against dead mussel in stagnant water

As in the preceding experiment the strength of the current was a factor too unstable to express its influence in figures the experiments were repeated in stagnant water. In an asbestos concrete container 6 rows of 12 mussels were glued on in the same way as described under 5, 36 living and 36 dead ones, with a mutual distance of about 6 cm. Between these 55 test mussels were set out.

Series	Number of test mussels	Living mussel		Dead mussel		Indifferent	
		alone	arrived later	alone	arrived later	alone	arrived later
1	55	18	–	7	–	30	–
2	55	18	4	9	–	24	–
3	55	14	3	10	–	28	–
4	55	14	2	8	2	29	–
5	55	21	1	6	–	25	–
totals	275	85 (31%)		40 (14%)		136 (50%)	

The results are about the same as those obtained in running water. The living mussels attract more congeners than the empty shells. The number of indifferent animals is very great in this experiment too, even still greater than in the preceding one.

7. Group of stones with a smell over against a group of stones without a smell

According to experiments 1 and 3 a correlation exists between the circumference of an object and the number of mussels it catches. This creates the impression that the searching of the mussels is not "directed", but that merely chance determines where they come to rest. On the other hand, we see from experiments 4 and 5 that mussels show an unmistakable preference for living congeners to dead ones. This cannot be the result of the large circumference of the living mussels, as living and dead mussels are equally large. From this we might be inclined to conclude that the searching mussels are attracted by the smell to congeners.

In order to examine the possible influence of the smell of mussels, but at the same time to exclude any other influence from the living animals, I took groups of stones, partly with and partly without mussel smell.

Five or six stones were glued on in the shape of a star on the bottom of an asbestos concrete basin and these formed a group; 25 of such groups alternated with 25 groups containing in their centre a cut off mussel foot, unattainable for the crawling mussels. The circumference of the "smell-group" measured on an average 1,4 times larger than that of the odourless group, due to the difficulty of making them equally large. Between the groups 36 mussels were set out.

Series	Number of test mussels	Group with smell		Odourless group		Indifferent	
		alone	arrived later	alone	arrived later	alone	arrived later
1	36	16	–	12	–	7	1
2	36	14	–	15	–	7	–
3	36	19	–	13	–	4	–
4	36	18	–	9	–	9	–
5	36	14	1	11	1	7	–
6	36	18	1	9	–	8	–
totals	216	99 (45,8%)		69 (31,9%)		42 (19,4%)	
7(!)	36	12	–	19	–	5	–
8(!)	36	9	–	18	–	11	–

Except in series 7 and 8, which are marked with (!), the mussel feet were always put on the same groups of stones. It is obvious that the preference for groups with a mussel smell was little at the start, but increased afterwards. When we take the results of series 1 up to and including 6 together we see that the numbers of mussels on the groups of stones with a smell are to those without a smell as 1,4 : 1. This is exactly the relation existing between the circumferences of "smelling" and "odourless" groups of stones.

Although the results of these series of experiments rather varied among themselves I had to break them off to find time for establishing in another way whether groups of stones smelling of mussels would perhaps be preferred to odourless groups. To that end musselfeet in series 7 and 8 were put on those groups that had remained odourless up to that time. If the searching mussels had been attracted by the musselsmell they would have had to follow the change and be numerous on the at first "odourless" but now "smelling" smaller groups of stones. Instead of this the number of mussels on the groups appeared to be more or less in proportion to the circumferences of these groups. We may thus safely assume a linear relation between the size of the circumference of the object and the number of mussels.

When we now add the results of series 7 and 8 to the preceding results and then calculate the totals and the averages, meanwhile taking into account that the numbers 12 and 7 have to change places with 19 and 18, we find:

Total number of test mussels	Group with smell alone	Odourless group alone	Indifferent alone
238	136 (47,2%)	88 (30,5%)	58 (22,4%)

The relation between the numbers of mussels on the groups of stones with and without a smell is 1,5 : 1, which deviates little from the relation between the circumferences 1,4 : 1.

8. Dead mussel over against dead mussel with foot press juice

The foregoing experiment showed that when variously sized groups of stones, partly with mussel smell and partly without are offered to young mussels, no influence of the smell on the settling animals can be proved. In the meantime the mussel smell may have an attracting influence all the same, which may be more or less undone by that of the larger size of part of the groups. The influence of the mussel smell ought to show more clearly then, when that of the larger circumference would be taken away.

In this experiment, therefore, 50 dead mussels instead of groups of stones were glued on, 25 of which were made "smelling" by means of press juice from mussel feet, whereas 25 were not. This was done by sucking up the liquid with a pipette and letting it run slowly over the glued on mussels. As the water was stagnant and was not moved by the pipette the juice remained lying closely round the mussels and could only spread by diffusion. Between the glued on mussels 36 test animals were set out.

To my great surprise 34 out of the 36 mussels were still in their places at the end of the experiment, whereas two had moved and were attached to a dead mussel without press juice. They were all lying on one side, their valves closed. It may be useful to remember that healthy mussels sit on the ventral side and have the valves opened.

In connection with this experiment the following one was carried out. In each of two equally sized glass vessels, filled with sea water to the same height, 8 mussels were set out at equal distances. To one basin press juice of mussel feet was added and stirred well through the water; the other remained without juice. After having been in the basin with pure sea water for 2 hours 7 mussels had crawled from their places, while some were sitting together; all of them had their valves wide open. In the basin with diluted juice 4 animals had remained in the same place, 2 were still crawling about and 2, which had crawled away at the beginning, were lying still; all of them held their valves closed. Without going further into this matter it is clear that the press juice affects the mussels in a very unpleasant way. Probably this influence is less noticeable in experiment 7, because the cut off foot was bleeding only a little.

9. Dead mussel over against living mussel without terminal part of the foot

We have seen the press juice to work paralysing rather than favourable, whereas cut off feet do not exercise a repelling nor an attracting influence. These facts do not explain why the mussels in experiments 5 and 6 show a marked preference for their living congeners to the dead ones.

As has been mentioned on page 19 all mussels were glued on with one valve, so that the living animals were enabled to project their foot and on one side to surround themselves with a number of byssus threads. Now, the presence of these tense threads might encourage the mussels to settle against a living congener rather than against a dead one lacking these threads. If, therefore, the mussels could be prevented from forming byssus threads the test mussels could not be influenced by these, in other words: an equally great number of test mussels ought to be found on both.

It is known that mussels attach themselves by first pressing from the protruded tip of their foot a liquid quickly hardening into the well known white disk, and after that, by means of the "heel" of the foot, attaching a byssus thread to the disk in question (HAVINGA, 1929, and WHITE, 1937).

In order to prevent the formation of end disks the tip of the foot of all living glued on mussels was cut off. Whether the lack of the tip, and therefore the impossibility of making a disk, also excludes the formation of byssus threads is uncertain; the result, however, was that during the experiment no more threads were formed. After the amputation the mussels mostly kept their valves closed for a few days. Healthy mussels have their valves wide open, especially in water poor in plankton.

After each series the disks and byssus threads were removed from each place where a mussel had been sitting. Next, the whole of the container was rinsed with alcohol and after every two series the living as well as the dead mussels were replaced by new ones, as this was easier than removing the byssus threads from their shells.

36 living and 36 dead mussels were glued on in 6 rows of 12; between them 55 test mussels were set out.

Series	Number of test mussels	Dead mussel		Living mussel		Indifferent	
		alone	arrived later	alone	arrived later	alone	arrived later
1	55	10	–	8	4	30	3
2	55	14	2	11	–	27	1
3	55	14	4	6	1	30	–
4	55	12	4	6	–	29	4
5	55	8	1	10	4	28	4
6	55	10	2	10	2	30	1
7	55	7	–	6	1	40	1
8	55	9	3	11	5	25	2
9	55	16	1	19	3	16	–
totals	495	100 (20%)		87 (17%)		255 (51%)	

In the beginning we see a preference for the dead to the living mussels, which are probably repellent because of the blood from the rest of their foot. During this time most of the injured mussels keep their valves closed; when these are opened again the wound on the foot is probably healed: about equal numbers reach the living and dead mussels now. The small number of test series, the strikingly high percentage of "indifferents" and the probably repellent action of the injured mussels must needs have a disadvantageous influence on the average values, but all the same we may probably conclude that a dead mussel attracts as many congeners as a living one without byssus.

10. Dead mussel over against living mussel without byssus

This experiment was a repetition of the preceding, but exacter, because now no foot was cut off. To prevent the mussels from spinning their byssus threads their whole ventral side was surrounded with a wall of celluloid glue. I succeeded in doing this in such a manner that the mussels could all the same open their valves for breathing, so that they remained alive. For a mussel which is forced to keep its valves closed dies within 2 or 3 days.

The dead mussels were glued on in the same way as the living ones; 25 dead and 25 living animals were glued on in 5 rows of 10. The number of test mussels amounted to 36.

Series	Number of test mussels	Dead mussel		Living mussel		Indifferent	
		alone	arrived later	alone	arrived later	alone	arrived later
1	36	5	1	8	1	20	1
2	36	7	–	8	–	20	1
3	36	11	1	7	3	13	1
4	36	6	2	6	–	21	1
5	36	8	–	9	–	18	1
totals	180	37 (20,5%)		38 (21%)		92 (51%)	

The result of this experiment proves – like the preceding – that a dead mussel and a living one which cannot form byssus are just the same to a searching animal; both attract an equally great number of test mussels. Just as in the experiments 4, 5 and 7 the number of indifferent mussels is very large. It is obvious that a searching test mussel easily passes by congeners when these do not occur in a group.

11. Stones with byssus over against stones without byssus

The preceding experiments have shown that dead mussels and living ones without byssus attract the same number of test animals. This does not yet show, however, that searching mussels prefer congeners with byssus threads, even though experiments 4 and 5 point in that direction [1]).

A repetition of these experiments did not seem advisable, nor a modification in such a way that the mussels would have to choose between living congeners with and without byssus. The great objection to experiments with solitary individuals was, moreover, that the result was unsatisfactory owing to the great number of indifferent animals. In order to make the best of the short time left to me I chose for a last experiment groups of stones, one half of which was to have byssus, whereas the other half was not. I had these byssus threads attached to the stones by mussels which were kept on them for 24 hours. After that they were carefully taken away so that the remnants of the threads remained on the stones. The arrangement consisted of 15 groups of stones with and 15 without byssus threads; those with byssus had a circumference on an average 1,4 times larger than the groups without. Each time 20 test mussels were set out between the groups. After each series the remnants of their byssus were scraped off from the stones which should have none, while after every two series these groups were taken to pieces and the stones cleaned separately. Finally the whole was rinsed with alcohol. The remnants of byssus were not removed from the stones which had byssus from the beginning.

Series	Number of test mussels	Group with byssus		Group without byssus		Indifferent	
		alone	arrived later	alone	arrived later	alone	arrived later
1	20	13	–	7	–	–	–
2	20	9	–	6	2	3	–
3	20	7	–	8	–	5	–
4	20	9	–	7	1	3	–
5	20	13	–	7	–	–	–
6	20	9	–	8	–	3	–
7	20	8	–	6	1	5	–
totals	140	68 (48%)		49 (35%)		19 (12%)	

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[1]) As already mentioned in experiment 3 remnants of byssus threads were for this reason carefully scraped off in those experiments in which a disturbing influence might be expected.

From these figures results that the numbers of mussels on the stones with and without byssus are related as 1,4 : 1 resp., a relation corresponding to that between their circumferences. So there is no question of the expected influence of the byssus threads. This may show that the tactile influence of an object with many angles surpasses that of a number of byssus threads. It should be added that naturally the byssus threads were not tense in the experiment, as they would have been under normal conditions.

Conclusions with regard to the laboratory experiments

These experiments show that young mussels released in shallow water on a hard bottom attach themselves preferably to other mussels. When the latter are solitary they have little chance to be found, whereas the chance is much greater when they occur in groups. From the fact that groups of stones attract more mussels the larger their circumference it is probable that the size of the circumference is most important here.

Living mussels attract more congeners than dead ones of the same size. As both are found according to chance and the numbers of mussels reaching them are apparently equal it is probable that dead mussels are less in demand for attachment than living ones.

I tried to demonstrate the influence of mussel smell on searching or settling mussels by experimenting with groups of stones and mussels made odorous by placing pieces of mussel feet on them or suffusing them with foot press juice. The results make it very probable that the juice has a harmful and repellent action, but that the mussel feet do not demonstrably influence the test mussels, presumably because the feet do not bleed much. The supposition that the mussels diffuse a smell, sooner inducing congeners to settle on them, is neither made probable nor improbable by the experiments.

When mussels are placed between dead mussels and living ones with their foot cut off, so that no threads can be spun, or between dead mussels and living ones withheld from spinning threads in another way, the numbers of animals reaching both these groups are about equal. This makes it probable that living mussels are not in demand over dead ones owing to a possible smell, but that the byssus threads may play a part in this preference for living to dead.

It was finally tried to make mussels choose between groups of stones with and without byssus threads, but a favourable influence of the latter could not be shown to exist. This does not prove that byssus threads are of no influence to mussels which want to attach themselves, but probably only that their influence is subordinate to that emanating from the stones themselves.

Recapitulating, the experiments make it probable that a mussel finds another by accident and that therefore the chance of meeting other mussels is proportional to the size of the circumference of their group. It is probable that smell plays no part in the attraction of congeners, but that, on the other hand, byssus threads are of some importance.

As to groups of stones and mussels it is not well possible to compare their influence on settling mussels. Only a comparison of the results of the experiments 1 and 2 as well as 2 and 3 gives us something to go by and tends to show that a group of stones with its angles and hollows is about as favourable to the young mussel going to attach itself as a group of congeners. From this it may be concluded that contact stimuli furnished by surfaces are apparently more important than those resulting from the presence of byssus threads.

VI. OBSERVATIONS ON THE FORMATION OF GROUPS OF MUSSELS

The observations made until now refer to the way in which mussels attach themselves to the substratum and the demands they make upon the latter. These are indirectly connected with the formation of mussel banks. The following observations relate more directly to the formation of such beds. Partly they are concerned with direct observations on crawling animals, partly with the growth of groups of mussels in running water without any attention being paid to the crawling mussels themselves.

1. The crawling of mussels

Direct observations on crawling animals were chiefly made with the aim of getting more certainty about the question whether mussels, when searching for a place to attach themselves,

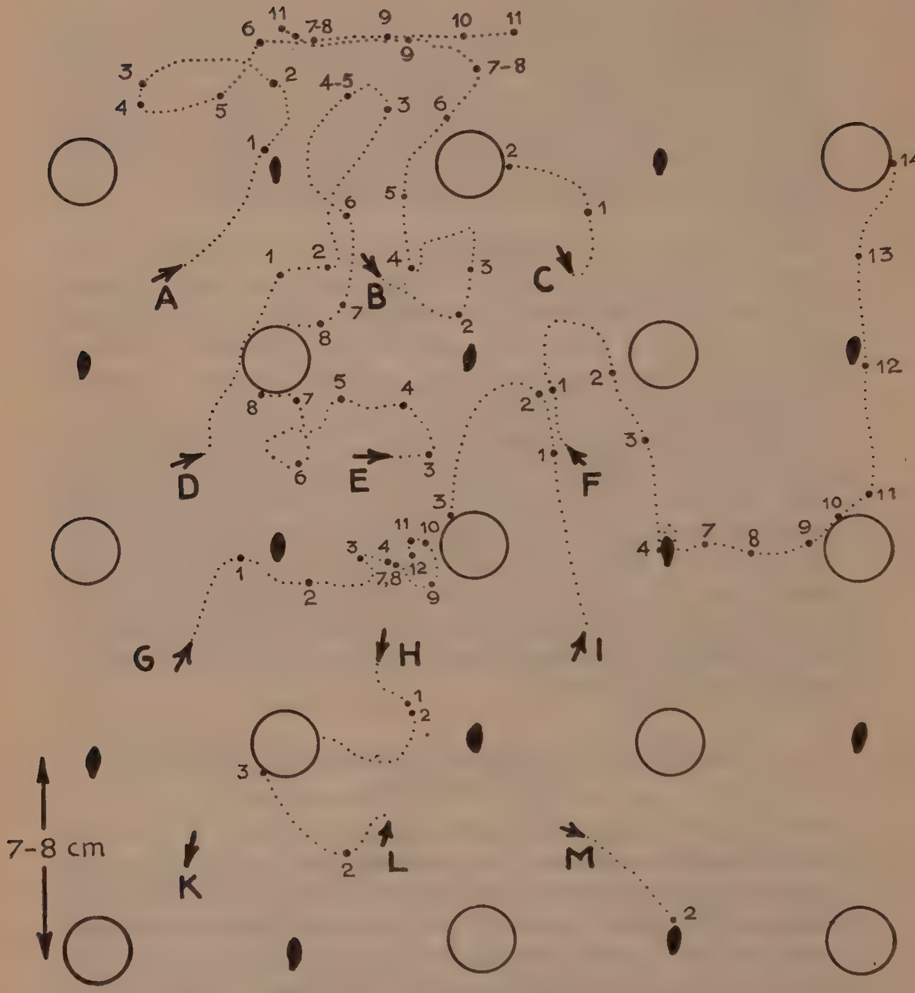

Fig. 4. The crawling of the young mussels. Oblong dots represent solitary mussels, circles groups of these glued on to the bottom. The test mussels have been denoted by letters (A, B, C, etc.). Figures denote 10 minutes time signals.

are chemically directed by congeners or not. The crawling was observed in a container in which, as in former experiments, other living mussels had been glued on individually and in groups. The accompanying sketch, fig. 4, in which each group of mussels is indicated by a circle and each individual mussel by an elongated dot, serves as an illustration. The test mussels are indicated by letters and the arrow points to the direction in which they have crawled away. The relations of sizes and distances are more or less to scale. The position of the mussels was continually checked and every 10 minutes time signals 1, 2, 3, etc. were indicated.

It appears from the traces of the mussels that their crawling is wholly arbitrary. The mussels C, H, L and M reached a suitable place for attachment after 20 or 30 minutes without or with very short detours. The others took a much longer time; a few of these stopped altogether without having found a mussel or a group (A, B and G). D crawled quite closely past a group of mussels, but reached it only after more than 80 minutes. F found a single mussel after 40 minutes, crawled round it in 25 minutes and left it again. It passed a group and a solitary individual and reached another group after 140 minutes. This shows rather clearly that mussels do not find each other with the help of a chemical sense. Although various experiments show that the mantle margin and the tip of the foot are very susceptible to concentrated solutions of NaCl, KOH and bitter substances, and the possibility of the chemical perception of a congener need not be excluded, the observations on crawling prove that mussels are not directed chemically. In valuating these results it should not be forgotten that these mussels found themselves under conditions different from those in nature. Yet, the indoor conditions were in my eyes sufficiently comparable to those in the field to make the results conclusive.

If mussels are not able to find one another with the help of their chemical sense over distances as short as these we may exclude the possibility of mussel beds being formed in this way, as in the field much greater distances are involved.

2. The growth of groups of mussels in running water

Whereas the foregoing observations clearly show that the crawling of mussels is quite arbitrary and that most mussels continue crawling till they have come across a place suitable for

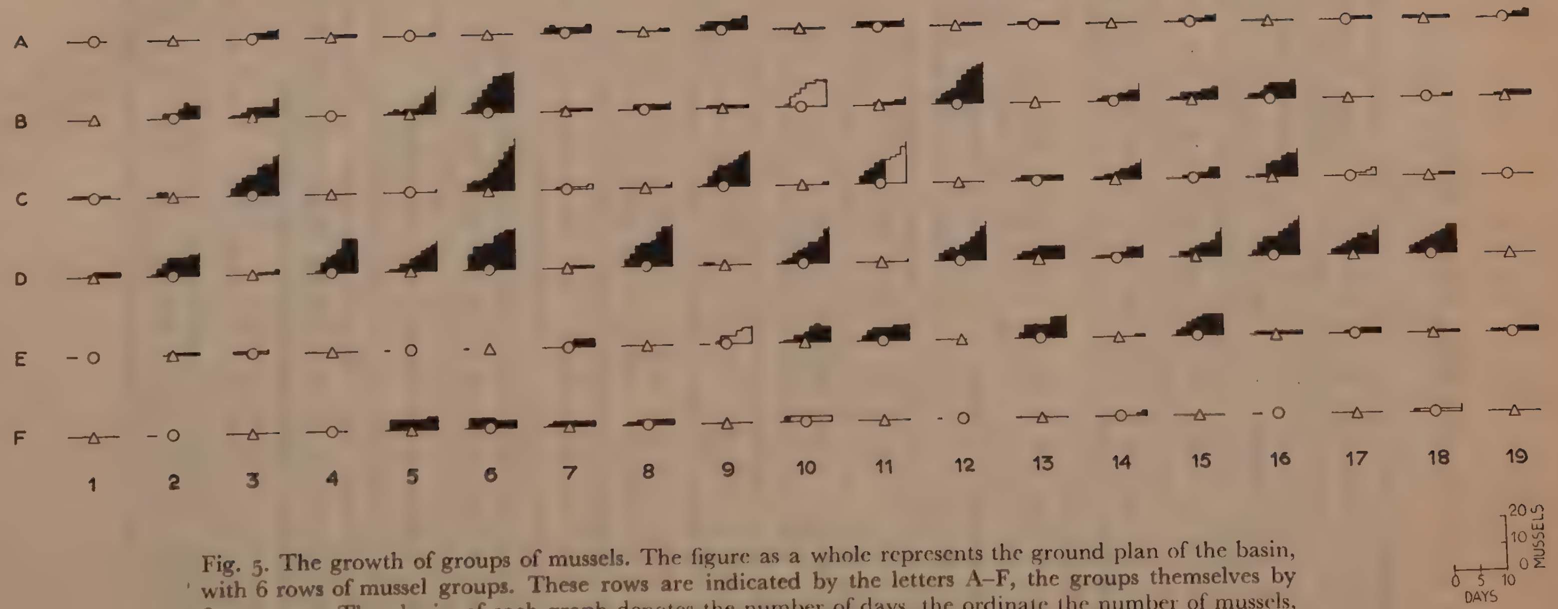

Fig. 5. The growth of groups of mussels. The figure as a whole represents the ground plan of the basin, with 6 rows of mussel groups. These rows are indicated by the letters A–F, the groups themselves by figures 1–19. The absciss of each graph denotes the number of days, the ordinate the number of mussels, as given in the separate scale. Circles represent groups of living, triangles groups of dead mussels. Black part of the graphs denotes up to which day after the beginning of the experiment the glued on mussels held out. For further explanation see text.

attachment the following experiments serve to gain an insight into the increase in size of the groups. In order to make conditions somewhat equal to those on the flats the experiment was carried out in running water in the same way as experiment 5 described above, with the only difference that the water was running very fast now. Here too the current could not be made equally strong over the whole section of the basin. Between B and D it was strongest, whereas outside the A-row, along the side of the basin, there was a counter-current. In the figure the current runs from left to right.

The "decoy" mussels were glued on in 6 rows; in each row a dead mussel – indicated by a triangle in the figure – alternated with a living one – indicated by a circle. Between rows B, C, D and E 51 mussels were set out every evening, without removal of the former ones, the positions of which were checked after 9 hours. After 10 nights the experiments were discontinued.

In the diagram (fig. 5) the absciss of each figure indicates the number of days during which the glued on mussel took part in the experiment. Some mussels got loose and this is indicated by breaking off the absciss. For instance, B 1 disappeared after the 6th night. The number of mussels which joined a solitary one is indicated by the ordinates; thus C 3 has caught 3 mussels after the 1st night, and after the 10th night there are 16. The apices of the ordinates are connected by a line and when the plane enclosed by this line and the absciss has been entirely blackened this means that the glued on mussel kept its place till the end. When the figure has been left wholly or partly blank it means that the glued on mussel disappeared after a certain number of days, but that on the same place test mussels settled all the same. In B 10 a mussel joined the glued on congener after the 2nd night; the latter disappeared after the 3rd night. The former remained, however, and new ones joined it. E 9 shows how the glued on mussel disappeared after the 2nd night and how in the 3rd night a new mussel arrived at the same spot, attaching itself to the remnants of the celluloid glue. Some figures show that sometimes mussels disappeared even from groups – B 5 and D 17 – but this is an exception. Finally in between the groups there were many solitary mussels which I did not figure for the sake of clearness and also because some of them changed their places and eventually joined a group. It was only rarely that these solitary mussels formed the starting point of a group themselves; this occurred at F 6 and 7, where a group of 3 mussels came into being. Further a group of 8 arose at F 11, groups of 2 and 4 between F 14 and 15, a group of 2 at F 18 and one of 5 between D 8 and E 9.

As might be expected the outer rows A and E gathered the smallest number of mussels, A however more than E, because of the strong counter current past A, which dragged the mussels along. These mussels near A, however, remained alone or formed only small groups.

Wherever the current was strongest – row A and B – the mussels on the left could not find hold, so that they landed near mussels or groups more to the right. In the fastly flowing water between A and D a cushion of dammed up water was formed to the left of each group of mussels to which the test animals dragged along by the current came rolling on, to slide downwards. The latter phenomenon, the strong current, the whirlpools, and the locally quiet water behind each object, all taken together, are factors which make it impossible to find for the left half of the basin a relation between the size of a group and the number of mussels it gathers. We rather find that these groups grow at the cost of the surrounding mussels or groups of mussels and most of all at the cost of those occurring downstream. The reason for this is that a crawling mussel only holds on with the tip of its foot, whereas the current especially has hold on the large surface of the valves. All mussels are thus more or less directed with the umbo against the current, so that they are forced to crawl upstream, at its most making a small angle with the direction of the current. The left upstream groups consequently get chiefly mussels from the right. The latter also include animals which first were dragged to the right by the current.

That one glued on mussel catches more test animals than another is partly accidental, partly due to the fact that mussels may leave a glued on congener again after having found it. A group once having been formed has more chance to catch mussels than a solitary individual, so that the advantage of the group over a single mussel becomes continually greater.

In the right part of the basin, where the water runs more quietly, the groups originate and grow more regularly.

It follows from these observations on the crawling of young mussels and the gradual growth of groups of such mussels under conditions imitating – if only in miniature – those in the field that the mussels reach congeners by means of the current more or less accidentally. This chance to meet other mussels is greater the larger the group formed by these; this we also found in preceding experiments. Applying this knowledge to what is probably taking place in the field the supposition is obvious that a mussel bank catches more mussels the more extensive its area. As a mussel bank can only develop into an extensive bed where the substratum is suitable for attachment, the number of mussels sufficiently large, and the current strong enough to transport them, the number of mussel beds on our coasts must be limited. For the rest one may expect all kinds of transitions from very large to very small banks, and this is what one actually finds in the fields.

VII. GENERAL CONCLUSIONS

Summarizing the results obtained, and especially referring to the question how the formation of mussel banks is brought about, we find the following.

It is probable that mussel larvae are extant everywhere in the water. Though no allusion was made to this fact previously it is of interest that mussels occur in great quantities on the hull of Dutch lightships lying some 20 km from the coast, far outside the area in which mussel beds are met with. This demonstrates clearly over what distances the larvae or young animals may be transported by the currents, especially as they do, of course, not cross such stretches directly.

There is little evidence for HOEK's supposition that spatfall chiefly takes place in areas eventually suitable for it by a concurrence of favourable conditions. Probably the spatfall is scattered over an extensive area.

At first the young mussels settle on all sorts of substrata, if these only give hold: a hard bottom, a ship's hull, a wooden campshot, stones, shells, sand tubes of the worm *Lanice conchilega* (L.), shells of *Balanus* species, but also algae, hydroid colonies, etc. The main condition is that the substratum is firm, and further that it is rough or contains corners, holes, cracks or grooves, in which the animals can attach themselves. While doing this they point the umbo downwards so as to have it as much as possible surrounded by the substratum. On the flats they often find this contact between umbo and substratum on the borderline between the latter and the surrounding sand. The umbo is there more or less sunk into the sand, whereas the sipho apertures, pointing upwards, remain free.

Very soon a great number of the young mussels do no longer hold on to the original substratum. It is probable that they leave it of their own accord and not because the current sets them free, for, as VERWEY told me, it also happens in places where the current is weak. This detaching probably takes place, because the substratum which once satisfied the thigmotactical needs of the recently metamorphosed spawn no longer satisfies the animals when they have grown somewhat older.

These detached young mussels are transported by the current and in such great numbers that we cannot but assume that they instinctively make this transport by the current possible. No observations or experiments on the actual transport, except those of NELSON mentioned on page 17, are known. It is, therefore, important that, according to my own observations, mussels may keep their foot projected while being dragged along by the current. When they come into contact with a firm object they immediately seize hold of it.

If the substratum reached after this transport is suitable for the young mussels they attach themselves. Probably they now make somewhat higher demands on the substratum than the first time and perhaps the hard objects on which they settle must be somewhat larger and the grooves which have to satisfy them somewhat deeper now. It is further probable that especially in the Waddenzee this attaching, detaching, and being transported by the current, is passed through by a great number of mussels a few or more times in succession before they have reached a substratum which will continue to satisfy them at a later age too. For it appears from KUENEN's and my own experiments that even mussels of a length of 5 cm, which must have an age of at least one year, are still transported by the current.

The substratum offering a sufficient hold to a full grown mussel must, besides being hard, preferably be provided with deep hollows. This kind of substratum is rare in an area as the Waddenzee with its sandy or muddy bottom. Properly speaking it is only supplied by cocklebeds which have been laid bare by the currents, and by musselbeds.

Probably, then, the reason why mussels congregate in such vast numbers is no other than that the mussel banks attract all the animals carried past on account of the structure of their surface only.

Consequently, everything points to the fact that the mussels do not find the mussel bed by chemoperception, but that they reach it more or less accidentally owing to these qualities:

1. to detach themselves when the substratum does not satisfy their thigmotactical needs;
2. to let themselves transport by the current so long as a suitable substratum is lacking;
3. to settle there where their thigmotaxis is satisfied.

It is obvious that some mussels will reach their purpose soon and that others will need a very long time and only reach a mussel bank when they have grown up to a fairly large size. The final result will be reached the sooner the greater the number of mussel beds in the area and the more extensive they are. It would be interesting to continue the investigations in this respect.

VIII. LITERATURE

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*) I did not read the original paper.

After I had finished the manuscript of this paper P. KORRINGA's Experiments and observations on swarming, pelagic life and setting in the European flat oyster, *Ostrea edulis* L. appeared in this periodical vol. 5, 1–249, 1941. It contains many points of interest in connection with my paper, to which it was too late to refer, however.

FENESTRA MEDIO-PALATINALIS UND INTERPTERYGOIDALSPALT

VON

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In einem vor kurzem erschienenen Lehrbuch hat einer von uns (VAN DER KLAAUW, 1941, S. 259) die Fenestra medio-palatinalis und den Interpterygoidalspalt begrifflich getrennt und dies nur mit dem folgenden Satz (in deutscher Übersetzung) begründet: „Da das Palatoquadratum in einem mehr ventralen Niveau als die Unterseite des Primordialneurokraniums zu liegen pflegt, kann man ausser den schrägliegenden Fenestrae medio-palatinales auch noch einen horizontalen Raum zwischen den medialen Rändern der beiden Entopterygoiden unterscheiden, den sog. Interpterygoidalraum, welcher bisweilen schmal sein kann und dann Interpterygoidalspalt heisst".

Es ist uns bekannt, dass diese begriffliche Trennung nicht üblich ist. Darum ist eine nähere Besprechung erwünscht, wobei uns auch die Möglichkeit gegeben ist auf die tieferen Gründe sowie auch auf die Bedeutung dieser begrifflichen Trennung näher einzugehen.

Die Benennung des sog. Interpterygoidalspaltes ist schon sehr alt. Die für uns so wichtige Arbeit von VERSLUYS (1912) entnimmt, dem Texte nach zu urteilen, diesen Begriff den Arbeiten NEWTONS, weshalb wir die betreffenden Stellen erst anführen wollen. Wir wollen aber die Bemerkung einschalten, dass reproduzierte Schädelabbildungen darauf hinweisen, dass dieser Name VERSLUYS auch von anderer, von ihm zitierter Seite bekannt gewesen ist. Siehe VERSLUYS Fig. D^2, welche BROWN (1905, Pl. III und S. 4, 8, 11, 22) entnommen ist. Wir weisen auch auf folgende von VERSLUYS (1912) angeführten Arbeiten hin: OWEN (1881, S. 94, 96, 100, 102, 103, Pl. 25, Fig. 1), ANDREWS (1896, S. 247 Fussnote, 251; dieser Arbeit entnimmt schon VERSLUYS, 1909, Fig. C den Name „interpterygoidaler Spalt"), SMITH WOODWARD (1902, S. 2, 5), WILLISTON (1902, S. 528, Pl. 2, Fig. 1), McGREGOR (1906, S. 43, 44, 84, 89) und ANDREWS (1910, S. 28, 81, 154, Fig. 47, 74).

Newton (1894 a, S. 479, 488) führt ein „median aperture of the palate" an, welche „occupies precisely the position of the interpterygoid vacuity" und in einer anderen Arbeit sagt Newton (1894 b, S. 578, 585) von den Pterygoiden eines anderen Fossils „leaving no indication of any inter-pterygoid foramen". Die Beispiele, welche Newton anführt, sowie auch die systematische Bedeutung der Grösse dieser Öffnung, worauf er hindeutet, machen es deutlich, dass er hier auf bekannte Sachen in der damaligen Literatur eingeht und auch keinen neuen Namen einführt. Wir werden hier nicht versuchen, ältere Literatur eingehend anzuführen und weisen nur auf Owens Handbuch hin (1866, S. 157, 158, Fig. 98 D; die „interpterygoid vacuity" ist unpaar; die paarigen Öffnungen beim Frosch, die „are divided from each other by the basisphenoid", nennt Owen „pterygo-maxillary vacuities", die den lateralen Gaumenlücken der Reptilia homolog sind; siehe S. 156, Fig. 98).

Versluys (1912, S. 613) führt in seiner Besprechung von *Pareiasaurus* erstgenannte Arbeit Newtons an und nennt die betreffende Öffnung „den interpterygoidalen Spalt" (siehe auch Fig. N, R, D^2). Und auf die zweite Arbeit Newtons hinweisend, sagt Versluys (1912, S. 644) von dem Schädel von *Erpetosuchus:* „In der Mittellinie des Munddaches liegt eine schmale, vorn bis zwischen die inneren Nasenöffnungen reichende Vertiefung, die wohl als ein interpterygoidaler Spalt (Deckenspalt) gedeutet werden muss". An anderer Stelle (1912, S. 629, Fussnote) sagt Versluys aber: „Die Bezeichnung 'interpterygoidaler Spalt' ist gewiss nicht schön, und ich werde daher denselben meistens 'Deckenspalt' nennen" (siehe auch S. 629, 630, 643, 644, 648, 667, 669, 673; Fig. F^2, J^2, W^2). An anderer Stelle (Fig. L) heisst er auch „Gaumenspalt". Versluys erwähnt an einigen Stellen, dass das Rostrum sphenoidale oder das parasphenoidale Rostrum in der Tiefe des interpterygoidalen Spaltes (oder Deckenspaltes) liegt (S. 613, 673). Auch sagt er, dass das Parasphenoid „in der Mitte des interpterygoidalen Spaltes" liegt (S. 603, Fig. O, Q).

Boas (1914), der mit der Mitteilung anfängt, dass von einer speziellen Behandlung der einschlägigen Literatur abgesehen wurde (S. 229), benutzt nur den neuen Namen Mediopalatinlücke. Bei den terrestren Wirbeltieren, wo Boas die Mediopalatinlücke unterscheidet, ist sie nach ihm dadurch entstanden, dass das Palatoquadratum „an einer begrenzten Stelle" (womit wohl die Basipterygoidverbindung gemeint ist) sich der Schädelbasis angelegt hat, wodurch „die grosse Spalte in zwei, die Mediopalatinlücke und die Pteroccipitallücke, geteilt wird" (S. 239). Mit der genannten „grossen Spalte" ist offenbar die breite Spalte zwischen der Schädelbasis und dem Palatoquadratum gemeint, welche bei den meisten Fischen besteht (S. 237, auch S. 232). Bei der Verbindung des inneren Randes des Palatoquadratums mit den ventralen Teilen des Schädels, die eine grössere oder geringere Ausdehnung haben kann, bleibt die Mediopalatinlücke als eine Lücke zwischen dem Sphenoid und dem Palatoquadratum übrig (S. 307). Die Mediopalatinlücke ist also im Prinzip eine paarige Lücke. Dies ist deutlich der Fall bei den platybasischen Stegocephalen und Amphibia. Ausdrücklich erwähnt Boas dies für die Gymnophiona; hier liegt „auf jeder Seite des breiten Parasphenoids die Mediopalatinlücke" (S. 243). Bei den tropidobasischen Schädeln ist der Sachverhalt weniger deutlich. Wir finden für diese Gruppen denn auch Beschreibungen, die auch eine andere Auffassung zulassen oder sogar andeuten. So sagt Boas (S. 260) bei der Besprechung der Cotylosauria, dass die Mediopalatinlücken „in der Mitte fast miteinander verschmolzen" sind, „indem der Teil der Schädelbasis, durch welchen sie getrennt sind, ganz schmal geworden ist" (in Fig. 38 fehlt diese trennende Schädelbasis) und für die Saurier erwähnt Boas (S. 267): „Die schmale Sphenoidalkante, welche die Mediopalatinlücken trennt, liegt manchmal, bei Betrachtung des Schädels von der Unterseite, etwas tiefer als die Palatoquadrata, so dass beide Lücken gewissermassen zu einer unpaaren zusammenfliessen". Die angeführten Ausdrücke „fast" und „gewissermassen" sind die letzten schwachen Hindernisse, in den genannten Gruppen die paarige Mediopalatinlücke dem unpaaren Interpterygoidalspalt gleichzustellen. An anderer Stelle (S. 264, 280) sagt Boas aber wieder deutlich, dass die schmale Basisphenoidkante bzw. das schmale Sphenoidalrostrum der Rhynchocephalia und der Ichthyosauria die Mediopalatinlücken voneinander trennt. In einer Anzahl von Abbildungen von der Schädelbasis fossiler tropidobasischer Gruppen fehlt die Basis des Primordialneurokraniums vollständig (Fig. 38, 74, vielleicht auch Fig. 75) oder ist nur ein kurzes Rostrum sphenoidale da, so dass die Lücke ungeteilt, bzw. nur teilweise paarig ist (Fig. 39, 63). Für *Loxomma* und *Pteroplax*, welche ventral gesehen bestimmt keine paarigen Lücken zeigen, sondern nur den einen unpaaren Spalt zwischen den Pterygoiden, erwähnt Boas (S. 241), dass die Mediopalatinlücken enge Spalten sind (die Bemerkung über *Loxomma* und *Pteroplax* ist ausnahmsweise der Literatur entnommen; Watson 1912, S. 8 nennt diesen Spalt „inter-pterygoid vacuity"; Boas' Fig. 62 ist nach McGregor 1906, der auch den Begriff „interpterygoid vacuity" auf S. 43, 44, 84 und 89 benutzt).

Der Name Mediopalatinlücke wird also von Boas nicht nur für den prinzipiellen Fall der paarigen horizontalen oder schrägliegenden Lücke zwischen dem Palatoquadratum und dem Seitenrande der Basis des Neurokraniums benutzt, sondern auch für den horizontalen Spalt zwischen dem linken und dem rechten Palatoquadratum. Dies geht auch aus der Vergleichung seiner Fig. 92 und 93 hervor (Querschnitt des Schädels eines Varans und einer *Boa* durch die Augenhöhle). Also können nach Boas die Mediopalatinlücken fehlen oder geschlossen sein, erstens dadurch, dass die beiderseitigen Palatina und Pterygoidea in der Mitte zusammengetreten sind, wie bei den Crocodilia (S. 275), zweitens auch dadurch, dass die Palatoquadrata sich der Unterseite des Schädels überall eng angelagert haben, wie bei Cynodontia, Schildkröten und Säugetiere (S. 281, 288, 299).

Die Angaben Abels (1919) in diesen Fragen können am besten für die Stegocephalen und Amphibia bzw. für die Reptilia gesondert angeführt werden.

Bei der Besprechung der Öffnungen des Stegocephalenschädels nennt Abel (1919, S. 249, Fig. 193, 228) die „Fenestra palatinalis (= Fenestra mediopalatinalis = Gaumengrube)", „die in der Mittellinie durch das Parasphenoid in eine rechte und linke Hälfte zerlegt wird". Mit dieser Ausdrucksweise werden die beiden Mediopalatinlücken von Boas als eine einzige Fenestra aufgefasst, welche in eine linke und rechte Hälfte geteilt ist, oder – können wir u.E. hinzufügen – geteilt sein kann, da es ja davon abhängt, ob die Schädelbasis im selben Niveau liegt oder nicht. So wird die Gleichstellung mit dem Interpterygoidalspalt vorbereitet, obgleich Abel diesen Schritt nicht macht. Bei den Stegocephalen spricht er nirgendwo von einem Interpterygoidalspalt. – In seiner Abbildung von *Ichthyophis* (Fig. 253) nach Boas heisst Boas' „Mediopalatin-Lücke" „Fenestra palatinalis".

Für die Reptilia gibt Abel leider keine derart einführende

Besprechung der Schädelöffnungen. Dies hat wohl zur Folge, dass er nur hier und da die Öffnungen im Texte bespricht oder nur in Textfigurerklärungen nennt, ohne zu einer einheitlichen Terminologie und einer begrifflichen Trennung zu kommen. Offenbar wird ABEL dabei sowohl von eigenen Auffassungen über die Stegocephalen, wie auch von denjenigen in angeführten Beschreibungen und Abbildungen früherer Autoren, geleitet.

Fangen wir die Besprechung der Textangaben ABELS mit dem komplizierten Falle von *Thaumatosaurus* an (S. 491, 495, Fig. 390). Hier sind die Verhältnisse deshalb so kompliziert, da „die Pterygoidea vor und hinter der durch das Parasphenoid zweigeteilten Lücke in der Mittellinie des Schädels zusammenstossen". Wir finden deshalb eine unpaare Öffnung, die mediane Lücke vorne zwischen den Pterygoidea (die Fenestra palatinalis anterior) und eine paarige Öffnung hinten, wo das Parasphenoid zwischen den Pterygoidea sichtbar ist und wo das Parasphenoid zwischen sich und den Pterygoidea „jederseits die 'Parasphenoidallücke' freilässt" (in Fig. 390 Fenestra palatinalis posterior genannt; dieser Name ist vielleicht unter Einfluss von ANDREWS, 1896, S. 247, 251 – siehe auch 1910, S. 81, Fig. 47, 74 – gebildet, der von „posterior palatine foramina" und „vacuity" spricht; siehe aber FRAAS, 1910, S. 127 Fussnote 2). *Thaumatosaurus* zeigt noch eine paarige Fenestra palatinalis: die Fenestrae palatinales laterales, die schmalen Lücken an den Grenzen von Pterygoidea und Palatina; diese sind wohl den lateralen Gaumenlücken BOAS' gleichzustellen. – Wir sehen also, dass ABEL einen neuen Namen einführt: die Parasphenoidallücke (siehe auch S. 498), ohne dies weiter zu begründen (WILLISTON, 1908, S. 716, 718, 719, 735 unterscheidet bei *Trinacromerum* „parasphenoidal vacuities" von „the (real) (true) interpterygoidal vacuity"; in Fig. 399 benutzt ABEL aber diese Namen nicht). Wir sehen auch, dass ABEL unter dem gemeinschaftlichen Namen Fenestra palatinalis verschiedene Öffnungen zusammenfasst; es gibt ja eine Fenestra palatinalis anterior, posterior und lateralis. Bei den Stegocephalen war, wie wir gesehen haben, der Begriff Fenestra palatinalis synonym mit Fenestra mediopalatinalis, bei den Reptilien ist dies also nicht der Fall. Zum Schluss ist bei ABEL (Fig. 344, 411) auch noch gelegentlich die Rede von einer Fenestra palatinalis mediana, welche man mit einer ungeteilten Fenestra palatinalis anterior und posterior gleichstellen könnte.

Dieser Name Fenestra palatinalis mediana ist wahrscheinlich dem Texte der Arbeit, in der sich eine der ursprünglichen Figuren vorfindet, und in der JAEKEL (1904, S. 183) die „lange spindelförmige Öffnung" das „mediale Gaumenloch" nennt, entnommen; an anderer Stelle spricht JAEKEL (1910, S. 219) nur von einer „Längsrinne, die von den inneren Flügeln der Palatina und Pterygoidea gebildet wird", ohne dieser Rinne einen Namen zu geben.

Die Bezeichnung Fenestra palatinalis oder palatina lässt es also unentschieden, welche Öffnung im Gaumendach vorliegt. In einigen Fällen zeigen die Abbildungen deutlich, dass die Fenestra palatinalis oder palatina eine Mediopalatinlücke BOAS' ist (Fig. 289, 357, 448). Auch Textangaben können eine Identifizierung einer Fenestra palatinalis mit der Mediopalatinlücke von BOAS sicher stellen, z.B. wo gesagt wird (S. 459), dass das Parasphenoid „die grosse Fenestra palatinalis teilt". – Eine Fenestra palatinalis kann im Prinzip aber auch eine laterale Gaumenlücke von BOAS sein. Dies ist sehr wahrscheinlich der Fall in Fig. 350 von *Champsosaurus*, wo die Textfigurerklärung meldet: „Orbita (von unten gesehen), unter ihr die Fenestra palatinalis", was wohl dem ursprünglichen Texte BROWNS entnommen ist, wo es heisst (1905, S. 8): „There is a large palatine foramen below each orbit". „Below" bedeutet hier nicht „unten in der Figur", sondern „mehr ventral" (siehe seine Taf. III). Eine Mediopalatinlücke ist damit bestimmt nicht gemeint, da BROWN auch das „interpterygoid foramen" oder „interpterygoid fenestra" kennt (1905, S. 4, 8, 11, 22, Pl. III). Dass ABEL von „Fenestra" statt von „Foramen" spricht, ist unwesentlich, da ja BROWN im Texte diese Öffnung nicht nur „palatine foramen", sondern auch „palatine fenestra" nennt (BROWN, 1905, S. 4, 8, 11). In anderen Fällen fügt ABEL aber das Adjektiv lateralis hinzu (Fig. 289, 411), nämlich bei Schädeln, bei denen entschieden eine laterale Gaumenlücke vorliegt. – Genau wie die Bezeichnung Fenestra palatinalis ohne weiteres für die komplizierteren Zustände bei den Reptilien unbestimmten Charakters ist, ist dies offensichtlich auch der Fall mit der blossen Bezeichnung „Gaumengrube". Bei den Stegocephalen war ja Gaumengrube synonym mit Fenestra palatinalis, d.i. mit der Fenestra mediopalatinalis (ABEL, 1919, S. 249). In der Abbildung eines Reptils, *Triassochelys* (Fig. 302) ist die „Gaumengrube" aber keine Mediopalatinlücke, sondern eine ventrale Schläfenöffnung oder Gaumenschläfengrube ABELS (S. 249), vielleicht kombiniert mit einer lateralen Gaumenlücke.

Fassen wir das von ABEL über die Mediopalatinlücke der Reptilien gesagte zusammen, so haben wir gesehen, dass fast überall von einer unpaaren Öffnung die Rede ist. Es handelte sich ja um eine durch das Parasphenoid in der Mittellinie halbierte Lücke, um eine mediane Lücke zwischen den Pterygoidea, um eine Fenestra palatinalis mediana, um eine durch das Parasphenoid geteilte Fenestra palatinalis. Nur beim Einführen des Begriffes Parasphenoidallücke, welche das Parasphenoid zwischen sich und den Pterygoidea jederseits freilässt, liegt der Gedanke einer paarigen Lücke nahe. Einige weitere Bemerkungen bei ABEL (S. 487, 495, Fig. 383), wo er die Mediopalatinlücke anführt ohne ihr einen Namen zu geben, sind damit im Einklang; hier wird gesagt, dass zwischen den Pterygoidea eine sehr schmale Spalte frei bleibt, woran im zweiten Beispiele hinzugefügt wird: „diese Spalte wird in ihrem hinteren Teile durch das langgestreckte Parasphenoid halbiert" (im vorderen Teile fehlt ja die Basis des Primordialneurokraniums). ABEL trennt also nicht bewusst eine paarige Mediopalatinlücke von einem unpaaren Interpterygoidalspalt. Nur in einer Figur (Fig. 270) erwähnt ABEL eine Fossa interpterygoidea; diese Figur ist aber VERSLUYS entnommen (1912, Fig. R), der hier von einem „interpterygoidalen Spalt" spricht (die Breite dieses Raumes war für ABEL wahrscheinlich Anlass hier von Fossa statt Spalt zu sprechen).

In einem Lehrbuchabschnitt verbindet nun VERSLUYS (1924, S. 313; 1927, S. 254) all diese Befunde und Benennungen. Für die Amphibia erwähnt er, unter Anführung von ABEL (1919) und BOAS (1914), die Fenestra palatinalis, welche als ein sehr weites Fenster medial von Pterygoid und Pars palatina bis an die Basis des Neurokraniums liegt; bei Gymnophiona, vielen Urodelen und einem Teil der Stegocephalen ist das „mediopalatine Fenster" schmaler. Bei den ältesten Stegocephalen, wo die Pterygoidea sehr breit waren, findet man an Stelle einer sehr weiten Fenestra palatinalis nur einen schmalen medianen Spalt (Munddachspalt oder interpterygoidaler Spalt) (1924, S. 320; 1927, S. 260). Bei den Reptilien lassen nach VERSLUYS (1924, S. 329; 1927, S. 267) die Pterygoidea nur eine schmale Fenestra palatinalis zwischen sich: den Munddachspalt oder interpterygoidalen Spalt, in dessen Mitte der schmale Unterrand des Septum interorbitale mit dem Processus cultriformis liegt Dieser Spalt kann lang oder kurz sein; dadurch, dass die Pterygoidea median aneinander anschliessen, kann der Munddachspalt sogar verschwinden. – Wir sehen also, dass VERSLUYS keinen prinzipiellen Unterschied zwischen einer paarigen Lücke und einem unpaaren Spalt macht und dass bei ihm Fenestra palatinalis, mediopalatines Fenster, Munddachspalt und interpterygoidaler Spalt entweder identisch oder durch allmähliche Übergänge miteinander verbunden sind. Wir wollen aber nicht weiter auf die zusammenfassenden Bemerkungen in dieser Arbeit von VERSLUYS eingehen, da dieser Autor 1936 eine eingehendere Zusammenfassung publiziert hat.

In seiner zusammenfassenden Bearbeitung des Reptilienkraniums nennt VERSLUYS (1936, S. 737) den schmalen Raum zwischen den Pterygopalatinspangen „Deckenspalt (VERSLUYS 1912) oder interpterygoidalen Spalt" und fügt hinzu: „BOAS (1914, S. 239) nannte ihn Mediopalatinlücke". Meistens gebraucht VERSLUYS in dieser Arbeit den Namen Deckenspalt(e) (S. 702, 737, 774, 777, 783; Abb. 523; 524, 564, 566). VERSLUYS (S. 699) nennt den schmalen Spalt zwischen den Pterygoiden auch wohl „Fenestra palatinalis oder Deckenspalt", an anderen Stellen heisst er „interpterygoidaler Munddachspalt" (S. 788, 801) oder „interpterygoidaler Deckenspalt" (S. 737). Der Deckenspalt ist also nach VERSLUYS eine unpaare Öffnung. Merkwürdigerweise sagt aber VERSLUYS auch (S. 737), dass bei den Reptilia der Deckenspalt „jederseits vom Rostrum sphenoidale nach hinten bis zu den Basipterygoidfortsätzen" reicht, was auf eine paarige Öffnung hinweist. Die relative Unabhängigkeit der Niveaux der Pterygopalatinspange und der Basis des Primordialneurokraniums wird dabei ausser Betracht gelassen. Dass dies VERSLUYS natürlich nicht unbekannt war, ist selbstverständlich, es geht ausserdem auch daraus hervor, dass nach ihm (S. 737, Abb. 566, 618) beim sekundären Verschluss oder bei der Reduktion des Deckenspaltes die sich ausdehnenden Pterygoide das Parasphenoid entweder zwischen sich fassen oder es von ventral her verdecken und von der Bildung des Mundhöhlendaches ganz ausschliessen.

Zum Schluss wollen wir hier die zusammenfassende Darstellung des Schädels der Stegocephalen und Amphibien von STADTMÜLLER (1936) aus demselben Handbuche besprechen. Bei den Stegocephalen nennt STADTMÜLLER (S. 509) das gut entwickelte, meist grosse und breite Fenster, welches das Os pterygoideum von der Gehirnkapsel trennt, und also u.E. als ein paariges Fenster betrachtet wird: Fenestra subocularis. Daraufhin folgt die Mitteilung, dass „eine ähnliche Fenestra oder eine Interpterygoidallücke" wohl von den ältesten Stegocephalen übernommen wurde (S. 509, Abb. 380). Es ist sehr wohl möglich, dass Stadtmüller Fenestra subocularis und Interpterygoidallücke nicht als identisch betrachtet, sondern die unpaare Öffnung mit dem Namen Interpterygoidallücke versehen will. Er erwähnt ja, dass bei den primitivsten Stegocephalen, in allerdings seltenen Fällen, die stark vergrösserten Pterygoide in der Mittellinie aneinander grenzen, „dabei fehlen Gaumengruben (Fenestrae suboculares oder Interpterygoidlücken) fast vollständig" (S. 513). An anderer Stelle bemerkt Stadtmüller (S. 603) von diesen Stegocephalen, dass sie einen geschlossenen, nicht fenestrierten, nur mit einer schmalen Interpterygoidlücke versehenen Gaumen besitzen. Sofort darauf folgt aber wieder eine Mitteilung (bezüglich der Dipnoi), woraus ersichtlich ist, dass Interpterygoidlücke und Fossa subocularis (Sewertzoff, 1926) einander gleichgestellt werden. Nun war nach Stadtmüller (S. 603) „bei den meisten (und typischen) Stegocephalen die Interpterygoidlücke grösser geworden und gab dem fenestrierten Gaumen mit divergierenden Pterygoiden (Abb. 381) den Ursprung (grosse Mediopalatinlücken Boas', . . .)". Auch hieraus wird es nicht deutlich, ob dadurch statt der unpaaren Interpterygoidlücke die paarige Mediopalatinlücke am Schädel, gerade ventral gesehen, auftritt. Diese Undeutlichkeit wird ebenfalls nicht aufgehoben in Stadtmüllers Auseinandersetzung der Ansichten Boas' in diesen Fragen über die „Mediopalatinlücke (= Gaumengrube)" u. dgl. (S. 606). In der Richtung der Auffassung der Mediopalatinlücke als eine paarige Öffnung weist vielleicht wieder die Bemerkung (S. 640/641), dass bei vielen Stegocephalen der Processus cultriformis des Parasphenoids sich zwischen den meist grossen Mediopalatin- oder Gaumenlücken nach vorn erstreckt. – Bei den Gymnophionen spricht Stadtmüller von den Mediopalatinlücken (S. 607, Abb. 442), ebenso bei den Urodelen (S. 612, 614, Abb. 461), bei den Anura von den „Mediopalatinlücken (Fossae suboculares, Sewertzoff 1926 b)" (S. 607, Fig. 426, 443, 444).

Es gibt noch mehr Benennungen der besprochenen Öffnungen in der Literatur, welche in den oben angeführten Arbeiten nicht benutzt werden, wie z.B. (siehe auch LAKJER, 1927, S. 63): Fenestra subocularis (GAUPP, 1893, S. 292, 315, 437, Taf. XIV, Fig. 13, 24; 1896, S. 37, Fig. 17; 1905, Fig. 366, 367; SEWERTZOFF, 1926, S. 80); Pterygoidspalte und Palatopterygoidspalte (BUSCH, 1898, S. 446, 448 usw.) und Vordermittelspalte (LAKJER, 1927, S. 63 usw.) [1].

Nach unserer Meinung hat man zwei Öffnungen im Mediananteil der Schädelunterseite [2] der Reptilia und Amphibia zu unterscheiden (siehe Fig. 1): 1. Den Interpterygoidalspalt, welcher zwischen den Medianrändern der Entopterygoidea liegt, sich aber auch zwischen denen der Palatina und Vomeres ausdehnen kann. Dieser Spalt ist unpaar, eine linke und rechte Hälfte liegen in einer einzigen „horizontalen" Ebene und er ist, wenn überhaupt vorhanden, ventral gesehen, immer sichtbar. – Jedoch wenn die Schädelbasis so weit ventralwärts reicht, dass sie den Raum des Spaltes ausfüllt, wird dieser geschlossen. Er kann auch in zwei Teile geteilt werden, dadurch, dass die – im Verhältnis zur Breite des Spaltes – relativ schmalere Schädelbasis so weit ventralwärts reicht, dass sie das Niveau des Spaltes erreicht oder sich sogar noch weiter nach unten ausdehnt. – Ist der Raum zwischen den Medianrändern der Entopterygoidea usw. breit, so mag es besser sein, statt von Interpterygoidalspalt, von Interpterygoidalraum zu sprechen. – Die Entwicklung des Interpterygoidalspaltes und -raumes ist vor allem wichtig für die Frage nach der Bildung des Munddaches.

2. Die Fenestra medio-palatinalis, welche zwischen dem Seitenrande der Basis des Primordialneurokraniums und den Entopterygoidea und Palatina liegt, hinten bis zur Basipterygoidverbindung, vorne bis zur Anheftung der Palatopterygoid-

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[1] Bei LAKJER ist der Vordermittelspalt eine unpaare Öffnung (S. 63, 183, 189, 230; Fig. 79–84), auch bei den Amphibia (S. 203). Nur an einigen Stellen könnte man meinen, dass nach LAKJER der Vordermittelspalt eine paarige Öffnung sei, z.B. wo er sagt, dass sie vom Rostrum parasphenoidale geteilt wird (S. 63, 74, 194, 203), trotzdem betrachtet LAKJER ihn als einen einzelnen Raum (S. 203).

[2] Die folgende Beschreibung und die Textfigur bezieht sich nur auf die Fälle, in welchen das Parasphenoid der Unterseite des Primordialneurokraniums eng angeschlossen ist und nicht breiter ist als diese Unterseite. In den Fällen, in welchen das Parasphenoid in deutlicher Entfernung von dieser Schädelbasis liegt oder (und) in welchen es breiter ist, sind die Verhältnisse komplizierter.

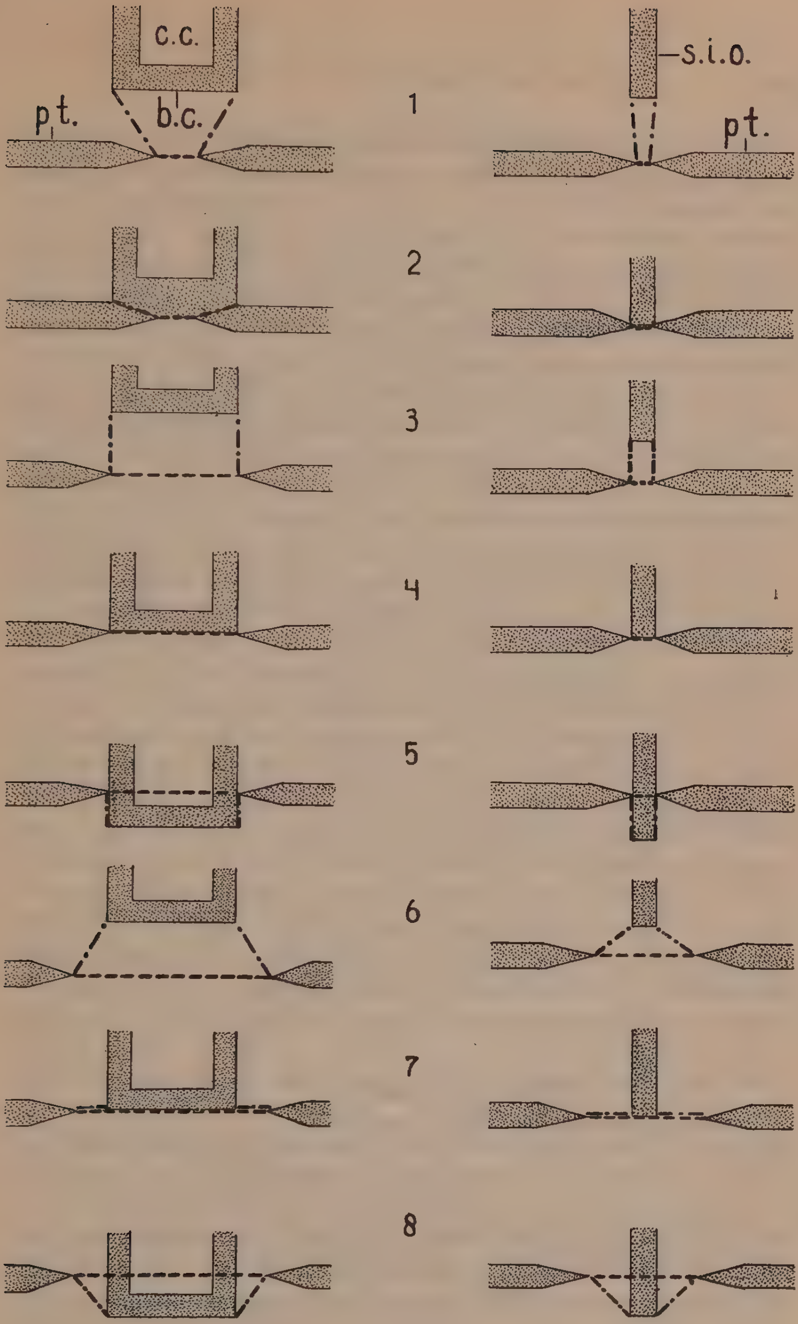

Fig. 1. Schematische Figuren zur Erläuterung der theoretisch möglichen Entwicklungsfälle des Interpterygoidalspaltes und der Fenestra medio-palatinalis; linke Abb. von platybasischen, rechte von tropidobasischen Schädeln. b.c. = Basis cranii; c.c. = Cavum cranii; pt. = Pterygoid; s.i.o. = Septum inter-orbitale; ----- = Interpterygoidalspalt; —·—·— = Fenestra medio-palatinalis.

spange an das Primordialneurokranium reicht. Diese Fenestra kommt paarweise vor, liegt meistens im Verhältnis zur Ebene des Interpterygoidalspaltes in einem schrägliegenden Niveau und ist, auch wenn vorhanden, ventral gesehen, nicht immer sichtbar. Letzteres ist der Fall, wenn der Interpterygoidalspalt schmaler oder genau so schmal ist wie die in einem mehr dorsalen Niveau liegende Basis des Primordialneurokraniums. Jedoch hat es auch in diesen Fällen Zweck, diese Fenestra zu unterscheiden, da sie ein Zeichen dafür ist, dass ein Raum zwischen der Basis des Primordialneurokraniums und dem Hauptabschnitt der Palatopterygoidspange ist, da dieser Raum eine Grundbedingung für die Kinese darstellt. – Ist der Interpterygoidalspalt schmaler oder genau so schmal wie die Basis des Primordialneurokraniums, und reicht diese Schädelbasis bis zum Niveau des Spaltes oder sogar noch weiter ventralwärts, so fehlt die Fenestra medio-palatinalis oder sie ist geschlossen. – Ist der Interpterygoidalspalt aber breiter als die Basis des Primordialneurokraniums, so ist im Schädel, ventral gesehen, die paarige Fenestra medio-palatinalis sichtbar; sie liegt in einem schrägliegenden Niveau, ausgenommen nur, wenn die Unterfläche des Primordialneurokraniums genau im Niveau des Interpterygoidalspaltes liegt. – Die Entwicklung der Fenestra medio-palatinalis ist also besonders wichtig in Beziehung zu den Fragen der Kinese und Akinese, zweitens auch in Beziehung zu den Fragen des Niveaus der Basis des Primordialneurokraniums und der Pterygopalatinspange und im Falle kinetischer Schädel auch in Beziehung zu Fragen der Neigung des Processus basipterygoideus. Letztgenannte Fragen stehen in Beziehung zu Fragen der Kinese und der Bildung des Munddaches, auch des weichen Munddaches.

Es muss noch hinzugefügt werden, dass es der Basis des Primordialneurokraniums entlang Unterschiede geben kann im relativen Niveau der Basis des Primordialneurokraniums und in der relativen Breite des Interpterygoidalspaltes. Ausserdem ist bemerkenswert, dass die Basis des Primordialneurokraniums teilweise knorpelig sein kann, so dass in trocknen Schädeln, nicht nur fossieler Formen, sondern auch rezenter, die Basis teilweise fehlen kann, wobei nur das Parasphenoid übrig ist.

Wir wollen in dieser Arbeit unbesprochen lassen, wie sich die genannten Sachverhalte in einer bestimmten Reihenfolge, z. B. phylogenetisch, ordnen lassen und wo sie vorkommen.

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ON TWO RHACOPHORUS SPECIES MENTIONED BY KUHL & VAN HASSELT

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In December 1820, H. KUHL and J. C. VAN HASSELT arrived in Java for studies bearing on the natural history of the East Indian Archipelago. Although both died within a short time of their arrival (KUHL on September 14th, 1821; VAN HASSELT on September 8th, 1823), they succeeded in bringing together extensive zoological collections, and in making numerous notes on the animals collected. The artists accompanying them (VAN RAALTEN, KEULTJES, BIK) made drawings of the species observed. The results of their studies they communicated in letters to C. J. TEMMINCK (director of the Leiden Museum), W. DE HAAN (curator of that museum), and to Prof. TH. VAN SWINDEREN (Groningen). Extracts from these letters were published in different journals. In a letter dated Buitenzorg, August 8th, 1821, KUHL & VAN HASSELT (1822a, pp. 103–104; 1822b, pp. 475–476; KUHL, 1824, pp. 370–371) describe the Amphibia, which they had observed during a trip to the top of Mt. Pangerango (W. Java). It is in this letter (1822a, p. 104) that they describe the genus *Rhacophorus* in the following words: "Twee heerlijke *Hylen* vonden wij aan den rand der Rosamalen-bosschen, onze *aurifasciata* en *chaleonotus* en twee andere nieuwe Kikvorschaardige Dieren, welke een eigen geslacht vormen, dat het naast bij de *Hylen* komt, maar door de vorming van den kop en huidige lappen tusschen den rug en de onderzijde der extremiteiten en door de geheele gedaante daarvan afwijkt. Wij noemen het geslacht *Rhacophorus*, Lappendrager, de eene soort *Reinwardti*, dewijl ook de Heer KEINWARDT dit dier gezien heeft, de andere soort noemen wij *moschata*, dewijl zij eenen sterken Bisamreuk zeer ver verspreidt." ¹)

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¹) WOLF (1936, p. 149) also cites this description in full, but as this was done from a copy written out by me, several errors (no doubt due to my bad writing) crept in, and, therefore, I thought it advisable to give the complete citation too. The german text (KUHL & VAN HASSELT, 1822b, p. 476) differs in some details from the dutch text, e.g., the "huidige lappen" (dermal flaps, in german: häutige Lappen) appear in the translation as "kantige Lappen", the specific name *reinwardti* is spelled "*Rheinwardti*" in

The generic diagnosis, although very short, is "as good as most of those given at that period" (M. A. SMITH, 1927, p. 213), and there can be no doubt as to the validity of the generic name *Rhacophorus* K. & v. H., 1822 (M. A. SMITH, l.c.; WOLF, 1936, p. 149). I cannot agree with STEJNEGER's argument (1907, p. 144) that the description was insufficient at the time of its publication, as any herpetologist receiving a specimen of *Rhacophorus reinwardtii reinwardtii* (Schleg.) from Java would certainly have recognized it as a species of the genus *Rhacophorus* K. & v. H. Another question is, however, whether the two specific names mentioned by KUHL & VAN HASSELT (*Rhacophorus reinwardti* and *Rhacophorus moschata*) are valid. One might reason, that both names are valid, as, besides the generic characters common to both species, the musk scent of *moschata* presents a character to separate the species from each other. Another possibility is to recognize *moschata* as valid, as one character is given for this species, while *reinwardti* is a nomen nudum. However, the two names are generally considered to be nomina nuda. Accepting this latter point of view, we have to deal with a case of a valid genus, which at the time of its original description did not contain valid species. Different cases of such genera have been dealt with in Opinion 46 rendered by the International Commission on Zoological Nomenclature (Publ. Smiths. Inst., no. 2060, 1912, pp. 104–107). None of the categories recognized in this Opinion agrees completely with the case of *Rhacophorus*, but the fourth category (genera based on a definite number of species not mentioned by name) comes nearest to the present case; the difference being, that for *Rhacophorus* two species are mentioned by names that are not valid. As stated in Opinion 46 one of these species must be the type of the genus. Therefore, the question arises, whether the two species mentioned by KUHL & VAN HASSELT can be identified. There can be no doubt that *Rhacophorus reinwardti* K. & v. H. is identical with *Hyla reinwardtii* Schlegel (1840?, pl. 30; 1844, p. 105), for SCHLEGEL (1844, p. 106) states that his *Hyla reinwardtii* had been discovered in Java by REINWARDT, and that it had been observed too by

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the translation; on the other hand the name of one of the "*Hyla*" species, viz., *chalconotus* is correctly written in the translation, while in the dutch text it has been misprinted. The french translation (KUHL, 1824, p. 371) mentions the dermal flaps as being present on the sides of the body; the specific name is written "*Reinwardtii*".

KUHL & VAN HASSELT. WOLF (1936, p. 147) fixed *Hyla reinwardtii* Schleg. as the type of the genus *Rhacophorus* K. & v. H.

The identity of *Rhacophorus moschata* K. & v. H. remained doubtful, however. WOLF (1936, pp. 150, 187) supposes that it may be identical with *Hyla margaritifera* Schlegel (1844, p. 107 note) (= *Rhacophorus schlegelii margaritifer* (Schleg.)), but recently I discovered that this is not the case.

Prior to his journey to Java, H. BOIE studied the javanese Reptiles and Amphibians for a prospected publication "Erpétologie de Java". When BOIE left Leiden in 1825, the manuscript was ready; in 1830 it was sent to the Imprimerie Normale at Brussels to be printed. Indeed part of it appears to have been printed. Our Museum possesses proofs of two plates, and one finished plate, but apparently nothing has been issued. On September 4th, 1841, TEMMINCK wrote to the Minister for the Interior, that at last the manuscript of BOIE (the first 44 pages lacking) and the drawings had been returned from Brussels; he mentions too, that the part which had been printed probably had been destroyed as a consequence of a seizure during the rise of the Belgians in the autumn of 1830 [1]). A number of the water colour drawings for the Erpétologie de Java were present in our Museum, together with manuscript notes, when in 1935 Dr. BOIE (Kiel, Germany) offered for sale to our Museum a number of water colour drawings from the inheritance of H. BOIE. These proved to be the drawings lacking from the set in our Museum, as could be checked from a list of the plates for the Erpétologie de Java. Among the drawings purchased in 1935 I found one sheet with a drawing of *Rhacophorus reinwardtii*. The inscription at the bottom of this sheet reads: "1. *Racophorus Reinwardtii*, 2. *Racoph. moschatus*", and it bears the signature "P. v. O." (= P. VAN OORT). Unhappily the upper half of the sheet with the figure of "*Racoph. moschatus*" had been torn off. A search for the lacking half of the sheet among the drawings already at Leiden resulted in finding the drawing of *moschatus*. The part of this half of the sheet that has been preserved fits exactly to the lower half, so that there can be no doubt that it indeed is the lacking figure. It had been cut out of the original sheet by SCHLEGEL, who intended to use it for a plate in his "Abbildungen" (1837–1844). An inscription in pencil in SCHLEGEL's hand reads: "*Racophorus moschatus*" of which the last word has been struck out, and has been replaced by "*margaritiferus* Boie" with a further annotation "v. OORT ad nat." In the manuscript notes by BOIE I found a description of *Racophorus moschatus*, which, although difficult to decipher (it is written in german characters with many abbreviations), undoubtedly refers to the frog shown in the drawing. This frog is certainly the *Hyla margaritifera* of SCHLEGEL (1844, p. 107 note), and so far WOLF's conclusion seemed to be correct. A further search in the archives of our Museum brought to light the manuscript notes made by KUHL and by VAN HASSELT in Java, as well as the drawings made by the artists accompanying them. Among these notes I found one leaf marked "*Racopherus moschatus* Nob" [1]), and which contains the description of a frog quite different from *Racophorus schlegelii margaritifer*. The description has been written by KUHL; the locality in which the frog had been taken is given as Aloun Aloun [2]), and a reference is made to a drawing ("tab nostra"). It is clear that this drawing to which KUHL refers cannot be the one, which was to have been used for the Erpétologie de Java, as the latter was made by P. VAN OORT, who together with BOIE left for Java on December 21st, 1825, about four years after KUHL's death. Moreover, VETH (1879, p. 38) mentions that the manuscripts and drawings of KUHL and VAN HASSELT reached Leiden on December 24th, 1825, three days after BOIE and VAN OORT had sailed. At first a search for the drawing referred to by KUHL was unsuccessful, but eventually I found a sheet marked "Mauvaises copies de dessins de VAN OORT etc." On this sheet one frog from Samao Id. (near Timor) is shown, and which probably was copied from a drawing by VAN OORT, who accompanied SALOMON MÜLLER to the eastern part of the archipelago in 1828–1829. Two drawings are copied from those made by one of KUHL and VAN HASSELT's artists (originals present), while the fourth drawing, according to the inscription, represents "*Rhacopherus moschatus* Aloen-aloen Java". The spelling of the name, as well as the locality are the same as in KUHL's notes. With this copy at hand, the original was easily traced. It had been cut out of the original sheet, and SCHLEGEL had used it as the fourth figure illustrating *Hyla reinwardtii* (SCHLEGEL, 1840?, pl. 30, fig. 4). That this is indeed the drawing to which KUHL refers in his notes is clear from the description, which exactly fits the specimen figured. The description reads as follows: "Color. Latere superiori et extremitatum latere angusto externo cum digito externo extremitatum omnium ex cano viridibus, obscure cinereo punctulato. Lateribus cum extremitatum pagina inferiori, digitis que omnibus, externo excepto, croceis, Labiis abdomineque albidis, collo infra luteo. Macula subaxillari et figuris pectoris marmoratis nigris. Palama inter 3 digitos antipedum inter 4 autem scelidum caeruleo nigroque variis. Iridibus cano argenteis. Pupila transversali horizontali, supra infraque emarginata. Dorsi tuberculis nullis."

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[1]) VETH (1879, p. 79) mentions that the Erpétologie de Java was stopped after the first part had been issued. I have no knowledge of a first part ever having appeared, and I can find no references to it in contemporary literature. Therefore, I believe TEMMINCK's statement that it had been destroyed to be correct. SCHLEGEL (1826, 1827) published extracts from BOIE's manuscript.

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[1]) Originally the name was spelled *moschata*, but the last *a* has been changed into *us*.

[2]) Aloun Aloun = Aloen Aloen is a valley on the S.W. side of Mt. Gedeh, W. Java (Aardrijkskundig en Statistisch Woordenboek van Nederlandsch Indië, vol. 1, 1869, p. 17. Amsterdam, P. N. VAN KAMPEN).

The only difference between the description and the drawing is, that in the former the pupil is described as emarginated above and below (i.e., constricted in the middle, as shown in a sketch accompanying the description), while in the drawing the horizontal pupil does not show the emargination (constriction).

Thus from KUHL's description, and from the drawing we are now able to definitely identify the *Rhacophorus moschata* of KUHL & VAN HASSELT; it was based on a (probably young) specimen of *Rhacophorus reinwardtii reinwardtii* (Schleg.). It is certainly remarkable that the collections of the Leiden Museum do not contain any specimens of *reinwardtii* collected by KUHL and VAN HASSELT, but that two specimens of *Rhacophorus schlegelii margaritifer* (Schleg.) collected by KUHL and VAN HASSELT are present.

WOLF (1936, p. 150) considers KUHL & VAN HASSELT's statement (1822a, p. 104; 1822b, p. 476) concerning the musk scent of *moschata* as erroneous. WOLF believes that this scent was due to some other animal or to a plant. In this respect KUHL's notes may be of some interest, as he wrote: "Sie gibt einen erstaunend starken Bisamgeruch von sich, besonders wenn sie einige Zeit in einem Gefasse aufbewahrt worden u komt nun heraus, so ist d. Geruch sehr angenehm u stark, wird aber imer weniger u zuletzt fast unmerkbar". This would point to a definite observation on the subject. It is of course possible that Kuhl and Van Hasselt made an error, but it may be interesting to make the experiment again, so as to prove definitely whether (young) specimens of *Rhacophorus reinwardtii reinwardtii* give forth a scent of musk. Siedlecki (1909) in his account of the biology of *reinwardtii* does not mention this scent, nor was it observed by Jhr W. C. van Heurn (verbal information), who kept the species in captivity.

With regard to the name *margaritifer* (*Hyla margaritifera* Schleg.) Wolf (1936, p. 187 note) is in doubt, whether it was given with regard to the small dots on the back or with regard to the tuberculi above the vent. From a manuscript by Schlegel it is clear that the name was derived from the tuberculi.

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BEOBACHTUNGEN ÜBER MEDUSEN AM STRANDE VON KATWIJK AAN ZEE (HOLLAND) IN DEN JAHREN 1933–1937

VON

H. VAN DER MAADEN

I. EINLEITUNG

Vor einigen Jahren machte Herr Dr. G. STIASNY, Konservator am Rijksmuseum van Natuurlijke Historie, Leiden, mich auf die Wichtigkeit einer Reihe von täglichen Beobachtungen während einer längeren Periode über das Vorkommen von Quallen an der Holländischen Küste aufmerksam. Ich habe dieser Anregung Folge geleistet und habe fünf Jahre lang fast täglich das Auftreten der Medusen beobachtet. Hauptzweck der Beobachtungen war die Periodizität im Auftreten der Quallen festzustellen. Es besteht über diesen Gegenstand ein kleiner Beitrag von VAN DEINSE (1924), welcher aber wenig detailliert ist. Weiter hat STIASNY (1930, p. 20), dem wir so viele Beobachtungen über Scyphomedusen verdanken, einige Tatsachen mitgeteilt, die ich weiter unten nennen will.

Meine Methode bestand darin, dass ich die am Strande angeschwemmten Quallen zählte. Ich bekam also nur einen Eindruck von der Anzahl, die vom Meer ans Land geworfen wurde, nicht von der im Meer anwesenden Anzahl. Es ist deshalb von grossem Interesse zu wissen in wie weit diese Zahlen vergleichbar sind. Aus den weiter unten gegebenen Einzelheiten geht hervor, dass der Wind – wie auch zu erwarten – grossen Einfluss auf das Anschwimmen der Medusen ausübt, mit andern Worten: es besteht kein direkter Zusammenhang zwischen der Häufigkeit im Meer und auf dem Strande. Nur dies lässt sich sagen: wenn viele Quallen angeschwemmt werden, so müssen viele im Meer anwesend sein, wenn sie nicht anschwimmen, so können sie sich nichtsdestoweniger im Meer zahlreich vorfinden. Da der Wind aber selten sehr lange konstant bleibt, so beeinflusst dieser Umstand nicht die Periodizität im Auftreten der Medusen als ganzes genommen; die extremen Daten dieser Periodizität können im Meer aber sehr gut etwas früher bezw. später fallen als am Strande.

Die Beobachtungen wurden, soviel wie möglich bei Niedrigwasser, fast täglich vom Frühling 1933 bis Ende 1937 angestellt. Der Strand bei Katwijk aan Zee, wo sie ausgeführt wurden, erstreckt sich ungefähr NNO–SSW. Hier wurde die Anzahl, die über einen Abstand von 1 km, zwischen 600 m nördlich und 400 m südlich vom Strandpfahl 88 angeschwemmt wurde, gezählt und zwar soviel wie möglich über die ganze Breite des Strandes, sowie im Wasser in unmittelbarer Nähe, bis etwa 3 m von der Wasserlinie. Bei grossen Mengen (über 2000 pro km) wurden die Quallen nur über einen Teil des Kilometers gezählt und danach das Ganze geschätzt.

Die erwähnten Beobachtungen sind nicht schwierig anzustellen, wenn der Strand flach ist. Anders wird es, wenn durch anhaltenden östlichen Wind ein ziemlich steil abfallender Sandwall von ca 1–2 m Höhe, auf welchem fast keine Quallen liegen bleiben, in der Nähe der Hochwasserlinie gebildet wird. An solchen Tagen musste ich meine Beobachtungen auf der trocken gelaufenen Sandbank anstellen. Weil sich diese meistens nur über einen Teil des Kilometers erstreckte, war ich gezwungen die Gesamtzahl pro km zu schätzen. – Bei südwestlichem und nördlichem Wind entstehen Einbuchtungen des Meeres (holländisch: zwinnen), zwei bis vier pro km, welche schräg landeinwärts gerichtet sind. Diese erschweren die Beobachtungen; es kommt vor, dass an der Mündung und am Ende solcher Einbuchtungen sehr viele Quallen zusammen getrieben werden, während auf der Bank selbst wenige zu finden sind, vergleiche die Fig. 1. Wenn an solchen Tagen die Quallen zweier nebeneinander liegender Kilometer gezählt wurden, gingen die Mengen der pro km beobachteten Medusen bisweilen weit auseinander. Solche Tage

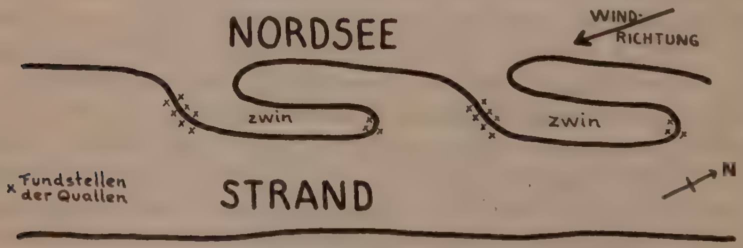

Abb. 1. Morphologie des Strandes, siehe Text.

kamen glücklicherweise nicht so oft vor und sie haben das allgemeine Resultat wenig beeinflusst.

So oft im Sommer die Garneelenfischer mit ihren Pferden die Netze (ein kleines Schleppnetz, holländisch: kornet) längs des Strandes zogen, wurde die Gelegenheit von mir benutzt, die Resultate meiner Strandbeobachtungen mit dem Inhalt dieser Netze zu vergleichen. Auch beim Schwimmen und Kanufahren sammelte ich einige Erfahrungen im Meere selbst.

Es ist mir eine angenehme Pflicht Herrn Dr. G. STIASNY, Leiden, und Herrn Dr. J. VERWEY, Direktor der Zoologischen Station, Den Helder, Dank zu sagen für ihre wertvollen Ratschläge und ihre Unterstützung bei meiner Arbeit. Auch meinen Freunden in Katwijk aan Zee, besonders Herrn H. BROUWER, die während meiner Abwesenheit die Beobachtungen fortsetzten, danke ich herzlichst.

II. BEOBACHTUNGEN

Die Wahrnehmungen beziehen sich auf die vier Medusenarten, die allgemein an der holländischen Küste vorkommen: *Cyanea capillata* (Linné), *Aurellia aurita* (Linné), *Chrysaora hysoscella* (Linné) und *Rhizostoma pulmo* (Macri). Sie sind wiedergegeben in den Diagrammen. Die Graphik der *Cyanea* enthält die Beobachtungen über das Auftreten der sogenannten Varietät *lamarckii* Pér. & Les. von *capillata* (L.), sowie der *capillata* selbst. ¹)

Die Kurven bedürfen kaum einer näheren Erklärung. Sie geben die Zahlen täglich pro km angespühlter Quallen, sowie die mittlere tägliche Windrichtung und -stärke, wie sie von mir selbst aufgenommen wurde, an. Tage mit fast völliger Windstille oder schwachem, veränderlichem Wind sind mit einer Wellenlinie angedeutet worden. Unter den Windkurven steht jedesmal die Windstärke angegeben und zwar in 4 Graden: schwach (Windstärke 1–2 DE BEAUFORT), mässig (3–4), kräftig (5–6) und Sturm (7–8 und höher). Die Zeit meiner Abwesenheit von Katwijk, während welcher ich keine genauen Angaben sammeln konnte, ist mit einer vertikalen, unterbrochenen Linie markiert.

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¹) Die Nomenklatur fusst auf der von MAYER in Medusae of the World, Vol. 3, 1910, gegebenen Synonymenlisten, wodurch die Namen mit den von VERWEY in seinem Beitrag in dieser Nummer der Archives benutzten übereinstimmen. Das systematische Verhältnis zwischen *Cyanea capillata* und der var. *lamarckii* habe ich schon in einem vorigen Beitrag (1942) besprochen.

Weitere Unterbrechungen in dem Winddiagramm deuten auf vereinzelte Tage, für welche ich keine Notizen besass.

Die Abbildungen zeigen, dass jede der genannten Arten eine deutliche Periodizität in ihrem Vorkommen innehält. Diese Periodizität wollen wir etwas näher betrachten.

Cyanea capillata (L.), einschliesslich der Varietät *lamarckii* Pér. & Les., erscheint im Mai. Ich besitze aber auch Funde aus März (17. und 18. III. 1935) und April (7. und 8. IV. 1934), während nach mündlicher Mitteilung Dr. STIASNYS 1939 schon am 5. Februar eine *Cyanea* in Katwijk gefunden wurde.[1]) Im Juni und Juli erreicht *Cyanea* ihre grösste Frequenz, um dann im August bis Ende September und sogar Oktober allmählich zu verschwinden.

Die einzelnen Jahre zeigen Unterschiede in der Zahl der Individuen und der Zeit ihres Erscheinens. Die Art war sehr zahlreich im Jahre 1935. Sie wurde in diesem Jahre auch früher in grösserer Zahl gefunden als in den anderen Jahren.

Die Varietät *lamarckii* kommt vom Februar an vor. Die früh im Jahr gefundenen Exemplare sind klein, meistens unter 10 cm. Während der Sommermonate kommen grosse und kleine durcheinander vor. Aus der Tabelle I geht hervor, dass die grossen Individuen am Anfang der Periode grösster Häufigkeit dieser Varietät relativ am zahlreichsten sind; später nehmen sie an Zahl ab. In dieser Anfangszeit sind sie auch am grössten; das grösste Exemplar (vom 14. Mai 1935) hatte einen Durchmesser von 28 cm. Exemplare, welche mit Sicherheit zu der *lamarckii*-Varietät gehören, habe ich nicht nach dem Monat August gefunden.

Cyanea capillata selbst wurde von Ende Mai an gefunden. Sie kommt viel weniger zahlreich vor als die Varietät *lamarckii* .Im Anfang ihrer Erscheinungsperiode fehlen die grössten Tiere. Diese erscheinen etwas später als die grössten der Varietät *lamarckii*. Am 1. und 14. Juli 1935 stellte ich als grössten Schirmdurchmesser einiger Exemplare 40 cm fest. Es sieht aus alsob die typische *capillata* relativ etwas später verschwindet als die Varietät *lamarckii*, besonders 1933 könnte darauf hinweisen. Der Unterschied ist aber jedenfalls weniger auffallend als aus STIASNYS Angaben (1930) hervorgehen würde.

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[1]) Auch am 15. Februar 1942 fand ich von dieser Art 2 Exemplare: 1 Ex. 35 mm. blau, 1 Ex. 23 mm. bläulich durchsichtig; am 29. März dieses Jahres wurde schliesslich noch ein blaues Ex. von 4 cm gefunden.

In Bezug auf die Färbung dieser Art möchte ich auf meine oben genannte Mitteilung (1942) hinweisen.

Aurellia aurita (L.) erscheint in etwas grösserer Zahl meistens etwas früher als *Cyanea capillata*: immer in der ersten Maihälfte. Frühe Daten für diese Art fehlen aber ganz, Daten vor dem Mai gibt es nicht. Auch ihr Maximum fällt früh, ungefähr eine bis zwei Wochen früher als das der vorigen Art, zwischen Ende Mai und Anfang Juli. Der Prozess ihres Verschwindens dauert bis in den September hinein.

Sehr zahlreich wurde *Aurellia* 1934 angeschwemmt, nicht im Jahre '35, dem Jahre in dem *Cyanea* zahlreich war. Das Maximum fiel 1935 früher als in andern Jahren, nichtsdestoweniger kam diese Art gerade '35 länger in den Sommer hinein vor.

Obwohl die Zeit des Auftretens von *Aurellia* und *Cyanea* grossenteils zusammenfällt, habe ich doch nie grosse Schwärme beider Arten zusammen auf dem Strande gefunden. Dennoch habe ich stark den Eindruck bekommen, dass grosse Zahlen beider Arten sich wohl gleichzeitig im Meer vorfinden können, aber wahrscheinlich nicht in denselben Wasserschichten.

Folgende Beobachtung weist darauf hin:

Den 7. Juli 1934. Nach einigen Tagen mit sehr wenig Quallen stellte ich um 6.15 Uhr 2 *Aurellia aurita* fest. Um 14 Uhr begegnete ich auf einer Kanufahrt, ungefähr 300 Meter vom Strande entfernt, Hunderten von *C. capillata* var. *lamarckii*; keine einzige *Aurellia* war darunter. Darum entschloss ich mich um 19 Uhr einen zweiten Beobachtungsgang zu machen. Zu meinem grössten Erstaunen zählte ich dann: *C. capillata* var. *lamarckii* ungefähr 50, *A. aurita* ungefähr 1500! Das Meer muss also am Mittag auch schon mit *Aurellia* bevölkert gewesen sein; weil ich aber an der Oberfläche nichts davon gesehen habe, befand sich dieser *Aurellia*-Schwarm wohl in den tieferen Wasserschichten.

Wie bei *C. lamarckii* können grosse Exemplare am häufigsten im Anfang der Zeit grosser Häufigkeit beobachtet werden. Am 24. Mai '35 fand ich ein Exemplar von 29 cm Schirmdurchmesser, am 28. desselben Monats eins von 34 cm. Im Gegensatz zu dem, was wir bei *Cyanea* sehen, geht dieser Zeit grosser Häufigkeit aber keine lange Periode geringer Häufigkeit voran, sodass grosse Tiere hier sogleich von Anfang an gefunden werden können.

Die *Aurellia*-Exemplare haben immer einen weisslich durchsichtigen Schirm, während Gastrovascularsystem und Gonaden weiss bis gräulichweisslich sind. Ein einziges Mal (23. Juni 1936) beobachtete ich einen Schwarm *Aurellia*, von denen Kanalsystem und Gonaden eine violette Färbung hatten.

Chrysaora hysoscella (L.) erscheint später, meistens nicht vor August. Nur zweimal fand ich sie im Juni, nämlich am 1. Juni 1935 1 Ex. von 20 mm im Pelagia-Stadium und am 20. Juni 1936 1 Ex. von 15 cm Schirmdurchmesser. Nur im Jahre 1937 beobachtete ich diese Art auch im Juli und zwar in bedeutender Anzahl, (siehe unten). Als Regel fällt das Maximum später, in die 2. August - bis 1. Oktoberhälfte. Nach Oktober werden die Tiere seltener. Zweimal habe ich sie noch bis in den Dezember hinein gefunden: am 3., 4. und 6. Dezember 1933 bezw. 18, 2 und 2 Exemplare, am 6. und 7. Dezember 1934 bezw. 2 und 1 Ex. Diese Beobachtungen stimmen in der Hauptsache mit denen STIASNYS (1927, p. 74) überein.

Die Art war offenbar zahlreicher im Jahre 1936 als in den anderen Jahren. Ihr Vorkommen fiel dieses Jahr ausserdem sehr spät, besonders wenn wir das Maximum mit dem aus dem Jahre '37 vergleichen. Nach STIASNY (1927, p. 73) war *Chrysaora* auch 1926 sehr zahlreich.

Grosse Exemplare können auch bei dieser Art am zahlreichsten im Anfang der Zeit ihres Erscheinens erwartet werden, also in der zweiten August- und ersten Septemberhälfte. Die grössten Exemplare fand ich am 15. Juli 1937. Als gewöhnlich grösste Schirmbreite dieser Art darf man vielleicht 20 cm ansehen. Aber an diesem 15. Juli wurde ein Schwarm angeschwemmt, der aus Exemplaren von abnormaler Grösse bestand. Die Schirmbreite der meisten Tiere war über 20 cm und mehrere Exemplare erreichten sogar eine Breite von fast 30 cm. Die Masse einiger Exemplare folgen hier:

Schirmdurchmesser 21.5, 22, 23.5, 24, 24, 25, 25 (Länge der Mundgardinen 75 cm), 26, 28 cm. Dieses Material befindet sich im „Rijksmuseum van Natuurlijke Historie" in Leiden.

Die Färbung und Sternzeichnung hat STIASNY (1927) ausführlich beschrieben. Meine Beobachtungen stimmen damit überein.

Rhizostoma pulmo (Macri) wird ebenso wie die vorige Art erst spät im Sommer, nicht vor August, gefunden. Das Maximum fällt in den September und Oktober, aber es werden noch im November Exemplare angeschwemmt.

Die Art war zahlreich im Jahre 1936 und besonders '37. Im Herbst 1938 war *Rhizostoma* während fast zweier Monate – September und Oktober – bei den verschiedensten Witterungen in grosser Anzahl am Strande zu finden.

Wie bei den vorigen Arten können grosse Exemplare am meisten zu Anfang der Zeit ihres Erscheinens beobachtet werden. Diese Erscheinung ist bei *Rhizostoma* zwar nicht so auffallend wie bei den andern Arten (grosse Exemplare können in bedeutender Anzahl auch im Oktober erscheinen), die grössten Stücke habe ich aber im Monat August gesehen. Der Schirmdurchmesser kann über 30 cm betragen. Als grösste Masse der Mundarme stellte ich am 27. August 1934 40 cm fest, Mundarme, deren Anhänge allein schon 15 cm lang waren.

Die Färbung ist meistens mehr oder weniger intensiv blau. Es kommen aber auch Exemplare mit bräunlicher, rostbrauner oder blass rotbrauner Farbe vor. Seltener ist die Farbe hell bis dunkelrosa oder sehr dunkelblau. Einmal, am 12. September 1936, habe ich einen Schwarm *Rhizostoma* von ungewöhnlicher Färbung beobachtet; die Exemplare, welche diesen Schwarm bildeten, hatten eine fast weisse Farbe mit bläulichem Stich. Die Randlappen sind nach meinen Beobachtungen jedoch immer dunkelblau.

Vergebens habe ich in allen Jahren auf *Pelagia perla* (Slabber) geachtet. SLABBER (1778, p. 109–110) hat diese Art einmal an der holländischen Küste festgestellt. Ich habe sie jedoch nie gefunden.

Nebenbei habe ich auch auf Ctenophoren und Hydromedusen geachtet, von denen ich nur eine kurze Übersicht über das Vorkommen vom Mai 1933 bis zum Januar 1938 gebe.

Ctenophoren

Pleurobrachia pileus (O. F. Müller) erscheint in ungeheuren Mengen (Millionen pro km) in der zweiten Hälfte des Mai bis Anfang Juni. Bis zum Oktober kann man dann noch Schwärme von bedeutender Anzahl beobachten. In den übrigen Monaten habe ich *Pleurobrachia pileus* auch gefunden, aber unregelmässig und nie in solchen grossen Mengen: im Januar, Februar und April 1934, Oktober 1936 und November 1937. ¹)

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¹) Sowie auch am 15. Februar 1942.

Hydromedusen

Eutonina indicans (Romanes) habe ich ziemlich viel am 1., 2. und 3. Juni 1934 und in geringer Anzahl am 11. Juni 1934 gefunden; 1935 erschienen einige wenige Exemplare am 25. Mai, 28. Mai und 1. Juni; 1936 einige am 17. und 20. Mai.

Eucheilota maculata (Hartlaub) kommt häufiger als die vorige Art vor; 1933: sehr viel am 25., 26. und 27. Juli; 1934: ziemlich viel am 2. August, sehr wenig am 28. August, zienlich viel am 6. und 7. September und sehr wenig am 29. September; 1936: zwei grosse Schwärme, und zwar vom 29.–31. August und vom 13.–17. September.

Von *Leuckartiara octona* (Fleming) habe ich einen kleinen Schwarm am 27. und 28. September 1936 beobachtet.

Aequorea forskålea Péron & Lesueur wurde im Herbst 1936 beobachtet. Einige Bruchstücke von Exemplaren dieser Art fand ich am 13. Oktober und 14. November, ziemlich viel am 3. Dezember dieses Jahres.

Das Material der gefundenen Hydromedusen befindet sich im „Rijksmuseum van Natuurlijke Historie" in Leiden.

III. RESULTATE

1. Periodizität und Häufigkeit

Was die Periodizität im Vorkommen betrifft, sind die wichtigsten Befunde der obigen Seiten in untenstehender Tabelle zusammengefasst:

Art	Hauptzeit des Auftretens	Jahre grosser Häufigkeit
Cyanea	Juni–Juli	1935
Aurellia	Ende Mai–Anfang Juli	1934 (und '38)
Chrysaora	Ende August–Anfang Oktober	1936
Rhizostoma	September–Oktober	1936–'37 (und '38)

Es fragt sich nun in wie weit diese Daten wirklich von Wert sind, in wie weit sie ein Bild der Periode grösster Häufigkeit auch im Meere geben.

Die Annahme liegt auf der Hand, dass das Anschwimmen bei den Quallen, genau wie bei zahlreichen anderen Meerestieren, stark von Wind und Strom beeinflusst wird. Bei der Küstenbevölkerung ist die Meinung verbreitet, dass Quallen besonders bei Landwind zu finden seien. Dies würde darauf hinweisen, dass sie mit dem Tiefenwasser ans Land gespült werden, denn bei Landwind wird das Oberflächenwasser vom Lande weggeweht und es entsteht ein nach dem Lande gerichteter Kompensationsstrom in der Tiefe. Ein Vergleich meiner Diagramme mit den Windangaben zeigt nun, dass hohe Maxima von *Cyanea capillata* bei SW, W, NW und N Winden, also bei Wind aus dem Meere vorkommen. Das bedeutet, dass die grossen Mengen dieser Quallen alle aus oberflächlichen Wasserschichten und nicht aus dem tieferen Wasser stammen. Das stimmt mit meiner Erfahrung überein, dass *Cyanea capillata* (sowohl *capillata* selber wie die Varietät *lamarckii*) oft erscheint nach einigen Tagen mit schönem Wetter bei östlichem Wind, nicht plötzlich in grossen Mengen, aber allmählich. Bei drehendem Wind wird diese Art dann plötzlich in grossen Mengen auf den Strand geworfen. Nach dieser grossen Zufuhr folgt fast immer ein schneller Fall der Zahl: das Meer wird gleichsam reingefegt.

Bei *Aurellia aurita* liegen die Dinge anders. Hohe Maxima kommen vor bei W, NW, N und NO Winden, ein einziges Mal auch bei SW und O Winden. Aber am meisten kann man *Aurellia* bei nördlichen Winden erwarten. Im Gegensatz zu dem, was wir für *Cyanea* finden, braucht nicht erst eine Periode von schönem Wetter mit östlichem Wind der Häufigkeit voranzugehen. Wenn im Mai der Wind nördlich ist, kann man im allgemeinen das Erscheinen von *Aurellia* erwarten ohne dass erst, wie bei *Cyanea*, ein östlicher Wind das Erscheinen der Quallen hervorgerufen hat. Man könnte hieraus schliessen, dass *Aurellia* im allgemeinen bei nördlichem Wind an der Oberfläche erscheint, um darauf mit dem Oberflächenstrom ans Land getrieben zu werden. Ich habe aber mehrere Male in solchen Perioden Mitteilungen von Küstenfischern erhalten, nach denen *Aurellia* auch zahlreich in Bodennähe anwesend war und zwar manchmal in solchen Mengen, dass das Fischen mit dem Schleppnetz fast unmöglich wurde. Es zeigt sich hieraus dass in einer *Aurellia*-Periode diese Art in allen Schichten des Meeres zu finden ist.

Was die beiden anderen Arten, *Chrysaora hysoscella* und *Rhizostoma pulmo*, betrifft, so ist die Sache etwas weniger deutlich. Das hohe Maximum von *Chrysaora* im Jahre 1936 fällt mit NW Wind zusammen, niedrige Maxima kommen aber auch bei SO Wind vor. Ich bekam den Eindruck, dass die Umstände, unter denen *Chrysaora* auftritt, ungefähr die gleichen sind wie die für *Cyanea*.

Bei *Rhizostoma* war es mir während der Beobachtungen ganz unmöglich einen Zusammenhang zwischen Anschwimmen und Windrichtung zu finden. Bei allen Windrichtungen fand ich sie in bedeutenden Mengen. Dies wurde mir besonders deutlich im Herbst 1938, als *Rhizostoma* während fast zwei Monaten – September und Oktober – bei den verschiedensten Witterungen in grosser Zahl am Strande zu finden war.

Wenn wir uns jetzt fragen in wie fern die Periodizität im Anschwimmen der Quallen einer wirklichen Periodizität in ihrem Auftreten im Meer entspricht, so ergibt sich, dass die Unterschiede zwischen den vier Arten nie dem Einfluss des Windes zugeschrieben werden können, denn alle Arten können von Winden aus der See ans Land getrieben werden. Da meine Methode aber nur ein indirektes Bild von den im Meer anwesenden Mengen gibt, so ist es selbstverständlich, dass die Zeiten des Auftretens im Meer sich nicht genau mit denen des Anschwimmens decken, so z.B. wird man die ersten und letzten Individuen am Strande selten zu Gesicht bekommen, und innerhalb der Periode des Vorkommens einer Art im Meer kann es sehr wahrscheinlich Tage geben, an denen kein einziges Stück angeschwemmt wird. Während an der Periodizität nicht zu zweifeln ist, ist sie also Jahr für Jahr nicht genau zu begrenzen.

Wie wir oben sahen, war *Cyanea* zahlreich im Jahre 1935, *Aurellia* 1934 (und 1938), *Chrysaora* 1936, *Rhizostoma* in den Jahren '36–'37 (und '38). Es wäre denkbar, dass dies dem Vorherrschen günstiger Winde in der Zeit des Auftretens der verschiedenen Arten in bestimmten Jahren zuzuschreiben ist. Aus den Windangaben geht aber hervor, dass wir diese Möglichkeit – jedenfalls der Hauptsache nach – ausschliessen können. Die Abb. 7 gibt in vereinfachter Form die Windverhältnisse für die verschiedenen Monate, in denen Quallen auftreten für jedes der fünf Jahre an. Ein Vergleich dieser Abbildung mit den Diagrammen und der Diagramme mit einander zeigt, dass Abwesenheit von Seewinden nur selten der Grund für das Fehlen von Medusen gewesen sein kann und umgekehrt kann auch ein Vorherrschen der Winde aus See nicht der Grund für eine grosse Häufigkeit der Medusen gewesen sein. In einem Fall, wie der vom Juni 1935, ist Zusammenhang zwischen dem Fehlen der *Aurellia* und dem Vorherrschen südwestlicher Winde denkbar, in vielen anderen sicher nicht.

Es geht hieraus hervor, dass die verschiedene Häufigkeit der Medusen, wie sie in den auf einander folgenden Jahren von mir am Strande beobachtet wurde, einer wirklichen Variation entspricht, die auch im Meer besteht. Das braucht uns übrigens nicht wunder zu nehmen, denn solche jährlichen Schwankungen sind bei Meerestieren sehr allgemein und auch für Hydromedusen auffallend, vergl. KRAMP, 1927, p. 222–223,

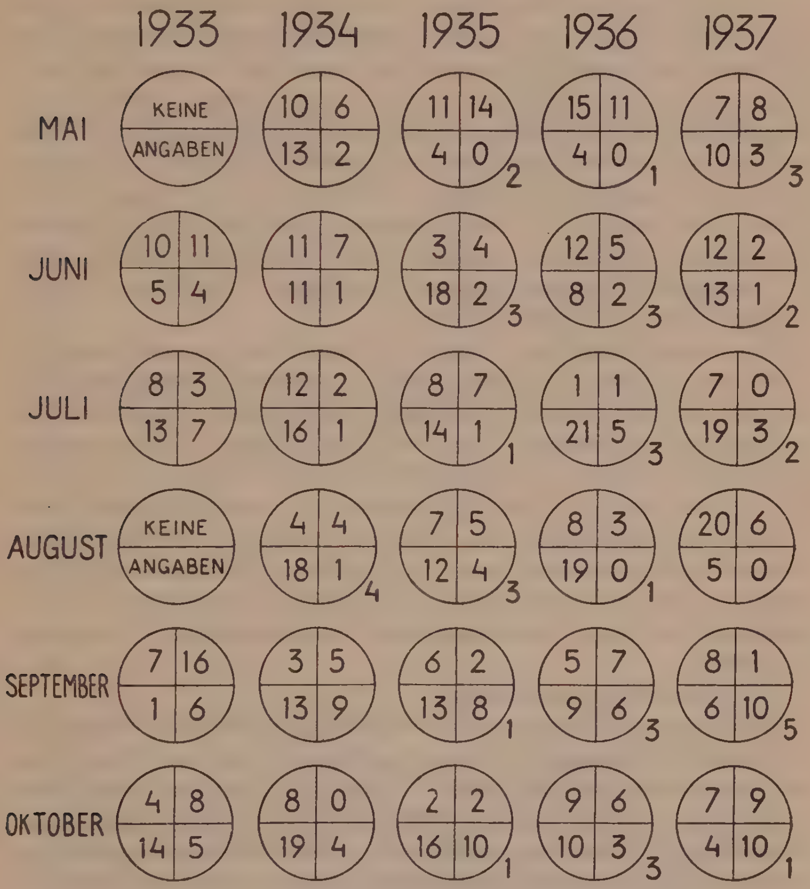

Abb. 7. Windangaben für jeden der Monate Mai bis Oktober in den Jahren 1933 bis '37. Jeder Quadrant links oben umfasst die Winde von WNW bis und einschliesslich N, jeder Quadrant rechts oben die Winde von NNO bis O, u.s.w. Die Zahlen geben die Zahl der Tage an, während denen der Wind aus dieser Ecke wehte; ihre Summe ist für jeden Quadrant also stets 30–31. Die Zahl der Tage mit Windstille oder mit schwachem, veränderlichem Winde wird durch Ziffern ausserhalb der Kreise angegeben.

und Russell, 1938, table I. Ausserdem wies Russell (1931) schon für *Cyanea lamarckii* darauf hin, dass sie deutlich zahlreicher war in den Jahren 1926 und '29, als '25, '27 und '30; Stiasny wies, wie gesagt, auf die Häufigkeit von *Chrysaora* an der holländischen Küste im Jahre 1926 hin.

2. Grössenunterschiede

Bei den verschiedenen Arten wurde darauf hingewiesen, dass grosse Exemplare einer Art relativ am meisten zu Anfang der Periode grösserer Häufigkeit zu finden und dass sie dann auch am grössten sind. So fand ich die grössten *Cyanea capillata* var. *lamarckii* Mitte Mai bis Ende Juni (die allergrösste Mitte Mai), die grössten *Aurellia* Ende Mai, die grössten *Chrysaora* im Juli, die grössten *Rhizostoma* im August; in dieser Zeit sind grosse Tiere ausserdem relativ am zahlreichsten. Nur von der typischen *capillata* findet man die grössten Tiere (Tabelle 1) nicht sofort zu Anfang der Periode grösster Häufigkeit, aber relativ etwas später als bei den andern Arten.

Es ist weiter auffallend, dass die Quallen, die sozusagen einen Schwarm bilden, das heisst die zusammen angeschwemmt werden, oft von ziemlich konstanter Grösse sind. Ein Schwarm *Rhizostoma* z.B. enthält Tiere, die zum grössten Teil entweder gross (über 20 cm), oder von mittlerer Grösse (10–15 cm), oder klein sind. Mehr oder weniger kann man diese Erscheinung bei allen Arten beobachten. Es wurde oben schon auf die enorme Grösse der Chrysaoren vom 15. Juli 1937 hingewiesen. Man gewinnt daraus den Eindruck, dass die angeschwemmten Tiere ungefähr gleichen Alters sind oder von demselben Geburtsort stammen.

3. Farbenunterschiede

Nicht nur die Grösse, auch die Farbe mag bei den verschiedenen Schwärmen einigermassen wechseln, so dass an einem Tag ein ziemlich konstanter Farbtypus auftritt. Ein Schwarm *Rhizostoma* z.B. kann entweder bräunliche, oder blassblaue, oder dunkelblaue Exemplare enthalten. Und auch dies gilt mehr oder weniger für die anderen Arten; oben wurden schon die Aurellien vom 23. Juni 1936, deren Kanalsystem und Gonaden eine violette Färbung aufwiesen, erwähnt. Die Erscheinung bildet wahrscheinlich eine Stütze für die Annahme, dass die angeschwemmten Tiere vom gleichen Geburtsort kommen können.

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TABELLE I

	Cyanea capillata *)		*C. c.* var. *lamarckii* *)		*C. capill.* oder *C. c.* var. *lamarckii*	
	Anzahl	Schirmbreite[1])	Anzahl	Schirmbreite[1])	Anzahl	Schirmbreite[1])
1933						
26–31 V	**4**	2½, 3, 4, 8	**23**	1½–9, 12, 15	**57**	2–8, 9, 10, 12, 14
1– 5 VI	**3**	?	**121**	2½–20	**103**	3–20, 22
6–10 VI	**105**	3, 4, 5–10, 15, 18, 18, 19, 20, 20, 23, 24	**22**	5–13, 15, 19	**65**	4, 5–16
11 15 VI	**59**	2½–12, 13, 18, 19, 22, 25, 30	**76**	5–14	**73**	2½–13, 14, 15, 16, 17
16–20 VI	**42**	3–15, 16, 19, 20	**858**	3–20	**41**	3–12, 15
21–25 VI	**5**	3–5	**166**	1½–10	**6**	2½–8
26–30 VI	**7**	6, 7–10	**628**	1½–10 (meistens 1½–6)	**18**	2½–6, 7
1– 5 VII	**14**	3–15, 19, 19, 20, 30	**100**	1½–7, 9, 10, 10, 16	**2**	4,12
6–10 VII	**17**	wenige klein, 10–15, 30	**910**	2, 3–17 (meistens 8–17), 18, 19, 20, 20	**41**	5–17 (Farbenvar. 5–10)
11–15 VII	**9**	2–10, 15	**34**	2–10	–	–
16–20 VII	**5**	5–7	**74**	2–10	**1**	6
21–25 VII	**1**	15	**4**	4–5	–	–
26–31 VII	**5**	ungef. 20	**42**	3–6	**1**	14
1– 5 VIII	–	–	**2**	5	**1**	10
6–26 VIII		keine Beobachtungen				
27–31 VIII	**7**	10–14, 15, 27	–	–	–	–
1– 5 IX	–	–	–	–	–	–
6–10 IX	**32**	13–20	–	–	–	–
11–15 IX	**24**	ungef. 15	–	–	**30**	?
16–20 IX	–	–	–	–	–	–
21–25 IX	–	–	–	–	**3**	?
1934						
7– 8 IV	–	–	**6**	5, 5, 8, 10, 10, 13	**15**	2, 3, 4–9
22 V	–	–	**1**	8	–	–
31 V	**1**	13	**1**	10	–	–
1 – 5 VI	**33**	9–20, 25, 25, 27	**15**	4, 7–12, 13, 15, 20	**9**	5–8, 12
6–10 VI	**1**	18	**5**	5–7	**5**	5, 7–10
11–15 VI	–	–	**2**	8–10	–	
16–20 VI	**5**	12, 12, 18, 20, 20	**650**	2–10 (meistens ungef. 5)	–	–
21–25 VI	–	–	**27**	3–10	**4**	5, 7, 9, 9
26–30 VI	–	–	**3**	4, 6, 10	–	–

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[1]) In cm.

	Cyanea capillata *)		*C. c.* var. *lamarckii* *)		*C. capill.* oder *C. c.* var. *lamarckii*	
	Anzahl	Schirmbreite	Anzahl	Schirmbreite	Anzahl	Schirmbreite
1– 5 VII	–	–	–	–	–	–
6–10 VII	–	–	**128**	4–14, 18, 20	**1**	10
11–15 VII	**4**	5, 10, 25, 35	**1204**	2–15 (meistens 5–10)	**41**	4–10
16–20 VII	**13**	3–8	**1514**	2–10, wenige bis 12	–	–
21–25 VII	**7**	5, 8, 8, 8, 12, 15, 22	**241**	2–10	–	–
10 IX	**1**	15	–	–	–	–
1935						
17–18 III	**2**	5, 9	–	–	–	–
11–15 V	–	–	**14**	5, 5, 8–10, 12, 14, 18, 18, 28	**15**	3–6
16–20 V	–	–	**87**	3–5, wenige bis 10, 15, 18, 20	**146**	3–5, wenige bis 10
21–25 V	**7**	4, 5, 7, 9, 11, 12, 13	**8**	7, 10–18	**12**	4–8, 10
26–31 V	**18**	4–11, 12, 17	**41**	4–16, 18, 18, 19, 20, 20, 20	**7**	4, 7–10, 11
1– 5 VI	**40**	1–5	**47**	1–5, 7, 7, 9, 11, 13	**2**	5
6–10 VI	–	–	**4**	?, 5, 10, 20	**1**	?
11–15 VI	ung. **28**	einige ?, 8, 12, 14, 15, 15, 19, 19, 20, 20, 22, 23, 24, 25, 25, 26, 30, 31, 35	ung. **434**	2–20	ung. **17**	2–10
16–20 VI	**3**	20, 20, 22	**2**	7, 12	**2**	13, 17
21–25 VI	**12**	13, 15, 20–25, 30, 33	**5**	5, 6, 8, 10, 10	–	–
26–30 VI	**8**	2–8	ung. **378**	2–15	ung. **22**	5–10
1–5 VII	ung. **325**	5–40 (meistens 20–30)	ung. **1739**	2–15	ung. **13**	3, 5–10, 18
6–10 VII	**1**	9	**70**	5–10	**10**	5–10
11–15 VII	**111**	5–40 (meistens 20–30)	**1580**	3–20 (meistens ungef. 10)	**57**	5–10, 11, 12
16–20 VII	**16**	3–9, 12, 18, 22, 23	**1918**	3–15 (meistens 5–10)	**1**	6–10
21–25 VII	**3**	2–5	**262**	2–12 (meistens 2–5)	**1**	ungef. 5
26–31 VII	**9**	4–10	**467**	3–14 (meistens 3–12)	**3**	5, 8, 10
1– 5 VIII	–	–	**29**	2–10	**1**	3

	Cyanea capillata *)		*C. c.* var. *lamarckii* *)		*C. capill.* oder *C. c.* var. *lamarckii*	
	Anzahl	Schirmbreite	Anzahl	Schirmbreite	Anzahl	Schirmbreite
6–10 VIII	–	–	**164**	2–12	**11**	?
11–15 VIII	**4**	? (2 grosse)	**170**	3–10 (meistens 3–8)	–	–
16–20 VIII	–	–	**2**	?	–	–
21–25 VIII	–	–	**12**	?, 6	**1**	?
1936						
5 V	–	–	–	–	**1**	10
15–20 V	–	–	**2**	8,9	**1**	8
21–25 V	–	–	–	–	–	–
26–31 V	**1**	10	–	–	–	–
1– 5 VI	–	–	–	–	–	–
6–10 VI	–	–	ung. **15**	2–8	–	–
11–15 VI	–	–	**1**	8	–	–
16–20 VI	**2**	7, 12	**2**	5, 8	–	–
21–25 VI	ung. **250**	10–15	**19354**	2–20 (meistens 5–10)	ung. **550**	5–10
26–30 VI	–	–	**60**	3–8	–	–
1– 5 VII	**2**	15, 25	**34**	5–10, 12, 12, 13, 14, 15, 15, 20	–	–
6–10 VII	–	–	–	–	–	–
11 VII	–	–	**1**	5	–	–
1937						
27 V	**1**	10	**125**	3–10, wenige bis 20	–	–
1– 5 VI	–	–	–	–	–	–
6–10 VI	–	–	ung. **110**	ungef. 10	ung. **14**	bis 10
11–15 VI	–	–	**21**	5, wenige ung. 10, 15–20, 25	–	–
16–20 VI	–	–	ung. **258**	meistens klein	–	–
21–25 VI	–	–	**178**	5–10, wenige bis ungef. 15	**5**	5–10
27 VI	–	–	**5**	5–10	–	–
8 VII	–	–	**1**	6	–	–
10–15 VII	–	–	ung. **150**	meistens 7–10	–	–
16–20 VII	ung. **10**	5–10	ung. **561**	5–10	**10**	5–10
21–25 VII	–	–	ung. **51**	klein	–	–
26–31 VII	–	–	**2**	5	–	–
1– 5 VIII	–	–	–	–	–	–
6–10 VIII	–	–	**264**	?	–	–
8 X	**1**	30	–	–	–	–

*) In dieser Tabelle sind nur diejenigen Tiere als *capillata* oder *capillata* var. *lamarckii* aufgeführt, die ich (hauptsächlich der Farbe nach) mit Sicherheit identifizieren konnte; alle unsichere Exemplare finden sich in der dritten Spalte. In den Diagrammen aber sind diese unsichere Exemplare zur einen oder anderen Art gebracht. Diagramme und Tabelle decken sich deshal nicht vollkommen, die Tabelle ist in dieser Hinsicht zuverlässiger als die Diagramme.

DIE PERIODIZITÄT IM AUFTRETEN UND DIE AKTIVEN UND PASSIVEN BEWEGUNGEN DER QUALLEN

VON

J. VERWEY.

ZOOLOGISCHE STATION, DEN HELDER

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I. EINLEITUNG

In den Jahren 1933–'37 sammelte VAN DER MAADEN, wie aus seinem Beitrag in dieser Lieferung der Archives hervorgeht, eine vollständige Reihe von Beobachtungen über die Periodizität im Erscheinen der Medusen in der Nähe von Katwijk aan Zee an der holländischen Westküste. Während der Ausarbeitung des Materials wandte er sich mit diesen Beobachtungen an die Zoologische Station, Den Helder, und dabei stellte es sich heraus, dass Katwijk und Den Helder offenbar Unterschiede in der Periodizität im Auftreten der Medusen aufwiesen. Das war für mich eine Anregung auch die Beobachtungen für Den Helder auszuarbeiten. Diese waren zwar sehr unvollständig; einige Gedankengänge, die grossenteils auf VAN DER MAADENS Beobachtungsmaterial fussen, machten die Sache aber interessant und so wird das Wenige dennoch publiziert. Hauptzweck für mich war, den Einfluss äusserer Umstände auf die Periodizität und auch auf die Bewegungen der Medusen kennenzulernen. Ich habe vor allem danach gestrebt auf Lücken in unseren Kenntnissen hinzuweisen; der Beitrag regt dadurch hoffentlich zu weiteren Untersuchungen an. Den Herren Prof. Dr. H. Boschma, Dr. C. O. van Regteren Altena und Dr. N. Tinbergen schulde ich vielen Dank für ihre kritischen Bemerkungen, die sie beim Durchlesen des Manuskripts machten.

Die Beobachtungen in Den Helder wurden nur ganz nebenbei während anderer Arbeiten gemacht und zwar in den Jahren '33 bis '39. Was Vollständigkeit anbelangt sind sie deshalb gar nicht mit denen van der Maadens vergleichbar. Die Mehrzahl bezieht sich auf viertelstündige Trawlfänge, die zur Aufnahme der Bodenfauna, und zwar der Hauptsache nach mit Schleppnetzen, gemacht wurden.

Die Netze unterschieden sich von gewöhnlichen Trawlnetzen darin, dass die Maschenweite von vorn nach hinten ganz regelmässig von 7.— bis 1.5 cm (Länge der gestreckten Maschen) abnahm. Ihre Breite vorn-oben war nicht genau die gleiche und betrug bei den drei benutzten Netzen resp. 14.3, 15 und 16.7 Meter. Auch die Längen und die Übergänge der Maschenweiten zeigten Unterschiede, was den Fang aber wenig beeinflusst haben dürfte.

Es versteht sich, dass diese Netze, die unmittelbar über (teilweise in) dem Boden fischen, zur Feststellung der im Wasser anwesenden Quallenmengen ganz ungeeignet sind. Dass die Fänge uns dennoch einigermassen ein Bild der Medusenverbreitung nach den Jahreszeiten geben können, beweist dass die Medusen sich ziemlich viel in der Nähe des Bodens (oder am Boden) vorfinden. Gefischt wurde mit einem kleinen, 13 m langen Motorkutter, dem Max Weber, und zwar, ausser bei Stillwasser, stets mit dem Strom. Beim Fischen bewegte sich das Schiff 1–1.5 km per Viertelstunde schneller als das Wasser, in einer Viertelstunde wurde meistens eine Strecke von 1–2$^1/_4$ km zurückgelegt [1]). Während die abgefischte Bodenstrecke also das eine Mal viel länger als das andere war, waren die jedesmal abgefischten Wassermengen etwas besser vergleichbar, da das Schiff ungefähr eine bestimmte Geschwindigkeit im Vergleich zum Wasser behielt. Die abgefischte Wasserstrecke betrug dadurch die vom Schiff in einer Viertelstunde minus die vom Wasser in Bodennähe in der gleichen Zeit zurückgelegte Strecke, was einen Abstand von etwa 1–1$^3/_4$ km ergibt.

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[1]) Man hat es in der Hand eine Kurre leichter oder schwerer über den Boden gehen zu lassen. Im allgemeinen wurde 3–5 Mal mehr Draht gefiert als die Tiefe betrug, in der gefischt wurde. Fiert man wenig und fährt das Schiff schnell, so geht das Netz leicht über den Boden, mit langen Leinen und bei langsamer Fahrt sinkt das Netz tiefer, wobei es schwer über den Boden schleppt. Dabei wird im ersten Fall natürlich eine grössere Strecke zurückgelegt als im zweiten. Schon die Länge der Leinen an sich beeinflusst, bei konstanter Tourenzahl des Motors, die Geschwindigkeit des Schiffes. Auch der Wind übt natürlich seinen Einfluss auf die Schnelligkeit der Fahrt aus.

Tabelle 1, zusammen mit der Karte in Figur 1, enthält eine Übersicht aller Fänge; ihre Anzahl ist klein, da in diesen Jahren vor allem mit dem Bodengreifer gearbeitet wurde. Die Aufnahme der Tabelle und der Karte hätte in diesem Beitrag unterbleiben können, findet aber statt, weil die Angaben auch für spätere Beiträge Wert haben.

Jeder Fang trägt, hinter dem Datum, eine Nummer. Die Liste der Beobachtungen (sieh unten) sowie die Karte enthalten die gleichen Nummern und man kann deshalb die in der Liste genannten Fänge mit Hilfe der Tabelle in der Karte finden. Die Römische Zahl hinter der Nummer gibt die im Journal der Station eingetragene Fangnummer an. Weiter enthält die Tabelle die Tiefenangaben für jeden Fang, ihre genaue Zeit und Dauer und die ungefähre Zeit des Hochwassers im Gebiet wo an dem Tage gefischt wurde. Daraus kann man ersehen ob zur Zeit der Beobachtungen Ebbe, Flut oder Stillwasser war und wie stark die Ebbe oder Flut ungefähr war. Die Dauer des Fanges betrug bisweilen nicht 15 Minuten, sondern mehr oder weniger. Kürzere Dauer kam selten vor, längere ziemlich oft, nämlich jedesmal, wenn der kleine Benzinmotor, der zum Einholen des Netzes benutzt wurde, nicht richtig funktionierte, was oft genug der Fall war. Einige Male (8. Mai '34, 5. Juni '35) wurden aber absichtlich längere Fänge gemacht.

Ein Sternchen neben der Nummer bedeutet, dass mit einem Netz, das nicht mit den drei regelmässig benutzten Netzen vergleichbar war, gefischt wurde. Meistens war dies ein von vorn bis hinten engmaschiges Netz von 11.5 m Breite und Maschen von 3.5–1.5 cm (gestreckte Maschen). Ein solches Netz fängt im allgemeinen (auch wenn man von der Grösse absieht) weniger als ein weitmaschiges, da es weniger Wasser durchlässt und mehr Wasser zurückwirft. Ich weiss nicht in wie weit auch die Quallenfänge von diesen kleinen Maschen beeinflusst wurden [1]).

Steht eine Nummer zwischen Klammern, so bedeutet das, dass der Fang misslang und die Zahlen deshalb nicht vergleichbar oder nicht brauchbar sind. Meistens war die Ursache, dass das Netz festlief und stellenweise zerriss; man beachte, dass einige der befischten Strecken eigentlich zum Fischen untauglich waren und von den Berufsfischern denn auch gemieden wurden.

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[1]) In den Fällen, in denen das Fischen mit einem solchen Netz stattfand, geschah das einige Male, weil die anderen Netze zerrissen waren (sieh unten), in den meisten Fällen aber in der Hoffnung bestimmte kleinere Tiere nicht zu verfehlen. Für den Fang kleiner Tiere kommt man nämlich nicht ohne ein solches Netz aus und die Nachteile müssen dann gegenüber dem Vorteil in anderer Hinsicht mit in den Kauf genommen werden.

TABELLE I.

Datum	Nummer	Fang	Tiefe	Zeit des Fanges	Zeit des Hochwassers	Cyanea	Aurellia	Chrysaora	Rhizostoma	Bemerkungen
21. Juli 1933	1	I	10–11	11.00–11.15	±7.00–8.00	zieml. viel	—	—	—	Bis 1936 grobmaschiges Netz, immer das gleiche, von dann an 3 solcher Netze benutzt.
	2	II	5.2–5.5	12.25–12.40		viel	2	1	1	
	3	III	20.5–21.2	14.30–14.45		110	4	2	35	
	4	IV	9.5	16.30–16.45		180	—	—	2	
28. Juli 1933	(5)	(Ia)	26	9.45–10.10	± 12.00	viel	—	—	5	Dauer 25 Minuten, Netz unklar.
	6	Ib	23–27	10.50–11.05		87	11	5	4	
	7	II	17–32	11.55–12.10		86	5	2	5	
	8	III	2.5–5	2 mal 7–10 Min.		—	—	4	—	
24. Aug. 1933	9	I	30–33	10.52–11.07	± 11.30	4	—	11	42	
	10	II	14–26	11.40–12.15		—	—	7	50	Dauer 35 Minuten, aber langsam.
	11	III	3–3.5	14.17–14.32		1?	—	—	4	
	12	IV	10–11	15.33–15.48		—	—	2	—	
	13	V	10	16.18–16.33		—	1	2	—	
	14	VI	8–8.5	17.12–17.27		—	—	1	2	
30. Aug. 1933	15	I	23–27	11.20–11.37	± 15.00	—	—	3	—	
27. Sept. 1933	16	I	28–29	11.20–11.35	± 14.00	—	—	—	1	
	17	II	27–28	13.06–13.21		—	—	—	—	
	18	III	26.5–28	13.53–14.08		—	—	2	1	
	19	IV	25–27.5	15.16–15.46		—	—	1	—	Dauer 30 Minuten.
10.–11. Apr. '34	20	I	10	18.00–18.20	17–18 U.	—	—	—	—	20 Minuten.
	21	II	11	19.10–19.25		—	—	—	—	
	22	III	9	8.50– 9.15		—	—	—	—	25 Minuten.
	23	IV	8	10.15–10.40		—	—	—	—	25 Minuten.
	24	Va	7	11.55–12.05		—	—	—	—	10 Minuten.
	25	Vb	4.5–7.5	12.35–12.50		—	—	—	—	
	26	VI	9	16.33–16.48		—	—	—	—	

	28	VIII	11	18.12–18.27		—	—	—	—	
	29	IX	11	30 Minuten		—	—	—	—	30 Minuten.
17. April 1934	30	I	21.5	10.27–10.42	± 9.00	—	1	—	—	
	31	II	20–21.5	11.15–11.30		—	—	—	—	
	32	III	16–17	12.28–12.43		—	—	—	—	
	33	IV	11–11.5	16.00–16.15		—	—	—	—	
	34	V	8–15	18.00–18.20		—	—	—	—	20 Minuten.
	35	VI	21.5–23.5	18.48–19.03		—	—	—	—	
8. Mai 1934	36	I	21–24	10.44–10.59	± 15.00	—	± 325 (5–20 cm)	—	—	
	37	II	21–25	12.21–12.51		1 (± 5 cm)	± 640	—	—	30 Minuten, aber langsam.
	38	III	10.5–11	14.16–14.31		—	± 125	—	—	
	39	IV	8–9.5	15.52–16.07		—	—	—	—	
	40	V	8	16.25–16.40		1 (klein)	—	—	—	
	41	VI	7–10	17.14–17.28		1	2	—	—	
	42	VII	± 10-± 20	20.50–21.50		—	—	—	—	Eine Stunde.
28. Mai 1934	43	I	31–33.5	10.37–10.52	8.00	2	—	—	—	
	44*	IIc*	25–27	15.37–15.52		2	—	—	—	Engmaschiges Netz.
15. Juni 1934	45	I	4–5	11.46–12.01	9.30	1	± 460	—	—	
	(46)	(IIa)	6.5–7.5	13.28–13.44		?	sehr viel	?	—	Netz so schwer von *Aurellia*, dass es zerreisst.
	47	IIb	6–7	15.02–15.10		1	± 25	1	—	8 Minuten.
	48	IIc	8–9	15.32–15.39		5	± 600	4	—	7 Minuten.
	49	III	6.5–9	15 Minuten		2	± 60	—	—	
	50	IV	3.8–4.5	18.37–18.52		3	± 40	—	—	
2. Aug. 1934	51	I	8–12	11.14–11.29	14.00	—	—	—	—	
	(52)	(II)	9–11	11.55–12.10		—	—	—	—	Netz zerreisst beim Einholen.
	(53*)	(III*)	20–22	12.43–12.58		—	—	—	—	Feinmaschiges Netz; zerreisst beim Einholen.
26. Sept. 1934	54	I	5–7	9.25– 9.40	± 11.00	1	—	2 (klein)	—	
	55	II	9.5–12	10.44–11.01		4	—	5 (klein)	—	
	56	III	9–12.5	11.42–11.57		—	—	15 (klein)	—	

TABELLE I (*Fortsetzung*).

Datum	Nummer	Fang	Tiefe	Zeit des Fanges	Zeit des Hochwassers	Cyanea	Aurellia	Chrysaora	Rhizostoma	Bemerkungen
28. Sept. 1934	57	I	2–9	9.34– 9.49	± 13.00	—	—	—	—	
	58	II	9.5–11	12.01–12.16		—	—	—	1	
	59	III	20–23	13.20–13.35		—	—	—	1	
	(60)	(IIIa)	18–22	14.39–15.04		—	—	—	—	Netz zerreisst beim Einholen.
	61*	IV*	8–11	15.47–16.02		—	—	—	2	Weitmaschiges Netz mit weitmaschigem Sack.
	62*	V*	19.5–22	16.35–16.50		—	—	—	—	Idem.
	63*	VI*	27–29	17.26–17.41		—	—	—	—	Idem.
	64*	VII*	19–21	18.12–18.27		—	—	—	—	Idem.
	65*	VIII*	4–7	19.01–19.16		—	—	—	1	Idem.
30. Mai 1935	66	I	5–9	9.50–10.20	± 18.30	2	25	—	—	30 Minuten.
5. Juni 1935	67	I	30	11.03–11.25	± 12.00	einige	einige	—	—	22 Minuten.
	68	II	11–19	13.10–13.32		einige	einige	—	—	22 Minuten.
18. Juni 1935	69	I	9–13	9.12– 9.27	10–11	—	20	—	—	
	70	II	8–11	9.54–10.07		1	11	—	—	
	71	III	15–20	10.58–11.14		6	29	—	—	
	72	IV	15.5–20	12.40–12.55		—	1	—	—	
18. Juni 1936	(73)	(I)	17–34	9.00– 9.34	± 6.30	2	4	—	—	9.00 bis 9.20 gefischt, dann mit Netz aus mit dem Strom getrieben bis 9.34. Netz kommt zerrissen oben. [Von diesem Datum an mit 3 grobmaschigen Netzen gefischt].
	74	II	5–6.5	10.33–10.48		2	51	—	—	
	75	III	12	11.42–11.57		—	—	—	—	
	76	IV	25–30	15 Minuten		—	—	—	—	

	77	V	5–7	16.33–16.42		6	18	—	—	Nach 9 Minuten festgelaufen.
17. Juni 1937	78	I	19	10.25–10.46	± 15.00	—	3	—	1	Gefischt 10.25–10.40, dann getrieben bis 10.46.
	79	II	10–14	11.30–11.50		—	2	—	1	Gefischt 11.30–11.45, dann getrieben bis 11.50.
	80	III	11–12	13.06–13.21		—	—	—	—	
	81	IV	4.5–13	14.10–14.25		—	39	—	—	
	82	V	5–6.5	15.05–15.20		—	22	1	—	
	83	VI	10.5–12	17.02–17.17		—	4	—	—	
23. Juni 1937	84*	I*	11.5–14	15.25–15.40	± 9.30	—	—	—	—	Engmaschiges Netz.
31. Aug. 1937	(85)	(I)	8			—	—	—	6	Netz 3 mal sogleich festgelaufen. Diese 3 Fänge zusammen genommen.
	86	II	14–14.5	13.30–13.45	± 18.30	1	—	—	5	
	87	III	13	16.35–16.45		—	—	—	7	Vermutlich schon 16.42 festgelaufen.
	88	IV	10	18.38–18.53		—	—	—	—	
17. Juni 1938	(89)	(1)	9–14	9.00– 9.15	± 12.00	—	—	—	—	Netz unklar.
	90	II	10–15	9.47–10.02		31	111	27	—	Schnelle Fahrt, Netzleinen kurz; Netz geht leicht über den Boden.
	91	III	9–13	10.35–10.50		88	396	7	—	Langsame Fahrt, Netzleinen lang; Netz geht schwerer über den Boden.
	(92)	(IV)	19–20	11.47–12.02		—	18	2	—	Netz unklar.
	(93)	(V)	17–22	13.12–13.27		1	—	—	—	Netz zerrissen.
	94	VI	29–31	14.22–14.37		2	7	3	—	
	95	VII	8–14	15.12–15.27		—	83	8	—	
	96	VIII	±10–16	16.31–16.46		1	9	—	—	
23. Juni 1938	97	I	10–11.5	9.51–10.06	± 16.30	4	19	7	—	
	98	II	16–17	10.30–10.45		6	10	2	—	
	99	III	24–25	11.45–12.00		kleine Anzahl	4	1	—	

TABELLE I (*Fortsetzung*)

Datum	Nummer	Fang	Tiefe	Zeit des Fanges	Zeit des Hochwassers	Cyanea	Aurellia	Chrysaora	Rhizostoma	Bemerkungen
23. Juni 1938	100	IV	21–25	13.34–13.49		6	8	3	—	
	101	V	25.5–26	14.37–14.52		6	40	1	—	
	102	VI	8	15.43–15.58		—	5	—	—	
	103	VII	10	16.34–16.49		3	6	5	—	
	(104)	(VIII)	19.5–20	17.28–17.43		—	—	—	—	Netz unklar beim Einholen.
27. Aug. 1938	105*	I*	10.2–14	10.12–10.27	± 11.30	—	—	—	10	Engmaschiges Netz.
	106*	II*	12.5–14	10.48–11.03		—	—	—	8	Engmaschiges Netz.
29. Aug. 1938	107*	I*	10–14	10.58–11.13	± 12.15	—	—	—	9	Engmaschiges Netz.
	108*	II*	7–15	11.53–12.08		—	—	—	24	Engmaschiges Netz.
	109*	III*	7–18	12.23–12.38		—	—	—	14	Engmaschiges Netz.
	110*	IV*	17–21	14.24–14.39		—	—	—	2	Engmaschiges Netz.
	111*	V*	11–16	15.15–15.31		—	—	—	—	Engmaschiges Netz.
	112*	VI*	8–20	16.00–16.15		—	—	—	—	Engmaschiges Netz.
30. Aug. 1938	113	I	10.5–12	10.28–10.43	± 13.00	—	—	—	147	
	(114)	(IIa)		11.15–11.30		—	—	—	—	Netz unklar.
	115	IIb	10.8–12	12.12–12.29		—	—	—	79	
2. Juni 1939	116	I	7–8	14.45–15.00	± 8.00	6	36	—	—	
27. Juni 1939	117*	I*	6–10	9.53–10.08		1	2	7	9	Engmaschiges Netz.
	118*	II*	6.5–11.5	11.12–11.27	± 17.00	8	13	7	2	Engmaschiges Netz.
	119*	III*	5–6	12.40–12.55		—	4	4	1	Engmaschiges Netz.
	120*	IV*	5–7	13.19–13.34		2	1	3	—	Engmaschiges Netz.
	121*	V*	5.5–8	15.30–15.45		1	—	1	—	Engmaschiges Netz.
	122*	VI*	15–17	17.51–18.06		2	7	14	—	Engmaschiges Netz.
31. Juli 1939	123	I	11–12.5	9.25–9.40	± 10.00	2	5	6	4	
	124	II	9–12	10.08–10.23		2	11	4	26	
	125	III	4.5–13	17.00–17.15		—	2	3	1	Engmaschiges Netz.
1. Aug. 1939	126*	I*	7–11	9.47–10.42	± 11.00	2	7	2	1	Engmaschiges Netz.

Ausser beim Fischen met dem Max Weber kamen Medusen auch bei anderer Arbeit zur Beobachtung. Im Hafen und in dessen Nähe (besonders der „Zuidwal" genannten Wattfläche entlang) wurde (am meisten in den ersten Jahren) mit einem kleinen Motorboot (holländisch motorvlet) mit einem kleinen engmaschigen Netz gefischt. Das Netz fing, vermutlich wegen seiner Kleinheit, sehr wenig Quallen; die betreffenden Fänge sind denn auch gar nicht mit denen des grossen Netzes vergleichbar und nicht in die Tabelle eingetragen worden. Es kamen die Tiere weiter im Oberflächenwasser zur Beobachtung. Besonders im Hafen wurden sie ohne weiteres an der Oberfläche gesehen oder vom Straminnetz gefangen, wenn es zum Planktonfang im Strom aushing. Auch auf dem Watt oder Nordseestrand südlich von Den Helder angeschwemmte Tiere wurden notiert.

II. BEOBACHTUNGEN

Die Beobachtungen beziehen sich auf 5 Arten: *Cyanea lamarckii* Pér. & Les., *Cyanea capillata* (L.), *Aurellia aurita* (L.), *Chrysaora hysoscella* (L.) und *Rhizostoma pulmo* (Macri) [1]. Von diesen wurden *Cyanea lamarckii* und *capillata* während der Beobachtungen nicht von einander unterschieden, da ich sie, Stiasnys Ansichten (1930) zufolge, für identisch hielt. Erst während der Ausarbeitung des Materials wurde es mir deutlich, dass wir zu dieser Annahme keinen Grund haben.

Cyanea lamarckii ist blau oder bläulich. Diese blauen Medusen bleiben kleiner als die braunen bis bräunlichen, nach van der Maaden (1942a) erreichen sie an der holländischen Küste meistens nicht mehr als 15 und höchstens 25 (einmal 28) cm [2]. Es gibt Zwischenstadien zwischen blauen und weissen Medusen, die, genau wie die blauen, nach VAN DER MAADEN selten über 15 cm Diameter erreichen und deshalb alle zu *lamarckii* zu rechnen sind. Die blauen Medusen werden schon bei 4 cm Durchmesser geschlechtsreif (ÖSTERGREN, 1909). Nach älteren Angaben [vgl. auch VANHÖFFEN, 1909 und '14 (STIASNY, 1930), ÖSTERGREN, 1909, KRAMP, 1937] haben die blauen Medusen weniger und kürzere Tentakel und kürzere Mundarme als die braunen, wenn gleich grosse Exemplare verglichen werden. Für eventuell weitere morphologische Unterschiede sieh STIASNY (1930). Sogar die Ephyren sollen etwas verschieden sein (HAGMEIER, 1930, KRAMP, 1937). Schliesslich reicht die Verbreitung dieser blauen Tiere von der englischen Südküste und dem Kanal bis in die dänischen Gewässer, vgl. KRAMP (1937). Nach DAMAS (1909) und KRAMP (1937) kommen die Tiere an der norwegischen Westküste bis ungefähr Bergen vor. Ihre grösste Häufigkeit erreichen sie in dem südlichen Teile der Nordsee (holländische Küste, Helgoland); an der holländischen Küste (VAN DER MAADEN, 1942a und b) sind die blauen Tiere viel zahlreicher als die braunen, in der Helgoländer Bucht sind sie die zahlreichsten Medusen überhaupt, in den dänischen Gewässern dagegen sind die braunen viel allgemeiner als die blauen.

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[1] Die Nomenklatur fusst auf den von Mayer in Medusae of the World, Vol. 3, 1910, gegebenen Synonymenlisten. Mayer behandelt *Rhizostoma octopus* (Gmel.) als Varietät der *Rhizostoma pulmo* (Macri.) Ich bin ihm hierin gefolgt. Es wäre aber der Mühe wert die Quallen der geographischen Varietäten dieser und einiger anderer Arten einmal unter gleichen Umweltbedingungen aufzuziehen, um festzustellen in wie weit die Unterschiede genotypisch festgelegt oder bloss phaenotypisch sind.

[2] In Plymouth erreichen die grössten Exemplare etwas mehr als 15 cm (Russell, 1931 b). „Die Durchschnittsgrösse der Helgoländer Exemplare dürfte 12 cm Durchmesser nicht überschreiten, über 15 cm grosse habe ich nie gesehen" (Hartlaub, 1896, p. 201). Nach Östergren erreicht sie (*C.palmstruchii*) an der schwedischen Küste einen Durchmesser von gewöhnlich 6–12, sehr selten von 15 cm. Mayer (1910, p. 597) gibt 30 cm als grössten Durchmesser an

Cyanea capillata ist braun oder gelb bis weiss. *Cyanea*s von dieser Farbe erreichen an der holländischen Küste nach VAN DER MAADEN bis über 40 cm Grösse. Sie sind offenbar erst bei einem grösseren Durchmesser (bei welchem?) geschlechtsreif. Es gibt Zwischenstadien zwischen braunen und weissen, wie es solche zwischen blauen und weissen gibt. Ausserdem gibt es eine kleine Anzahl braune Tiere mit ein wenig Blau und es sind diese, die das Erkennen beider Arten schwierig machen. Die braunen Medusen haben, auch wenn gleich grosse Exemplare verglichen werden, nach einigen Autoren (vgl. oben) stärker entwickelte Tentakel und Mundarme als die blauen. Die Verbreitung der braunen Tiere reicht von unserer Küste (wieviel südlicher?: Plymouth Marine Fauna gibt die Art nach Beobachtungen von BROWNE sogar noch für Plymouth an) bis tief in die Ostsee hinein, bis in den finnischen Meerbusen. Sie sind sehr zahlreich in den dänischen Gewässern, viel weniger zahlreich im südlichen Teile der Nordsee.

STIASNY (1930) hielt die blauen Medusen für das Jugendstadium der braunen. Meiner Meinung nach war nur eins der vier von ihm genannten Argumente stichhaltig, nämlich dass man nie kleine junge braune oder gelbe *Cyanea*s, sondern nur kleine blaue sieht. Aus VAN DER MAADENS Angaben (1942a und b) geht aber hervor, dass dem nicht so ist, dass im Gegenteil braune oder gelbe *Cyanea*s von 10 mm an an der holländischen Küste in ziemlicher Anzahl zu finden sind. VAN DER MAADEN kommt deshalb zu dem Schluss, dass wir, statt mit Altersstadien, mit Grössen- und Farbenvarietäten einer und derselben Art zu tun haben. Da nun aber die beiden Farbenextreme nicht nur von verschiedener Grösse sind, sondern auch verschieden früh reif werden und verschiedene Verbreitung haben, während diese Unterschiede auch nach VAN DER MAADEN sogar mit morphologischen Unterschieden einher gehen, wäre es unrichtig die Tiere als zu einer einzigen Art gehörig zu betrachten. Ich schliesse mich deshalb KRAMP (1937) an, der die Tiere als zwei verschiedene Arten betrachtet. Dieser hält weiter *C. palmstruchii* (Swartz) aus dem Skagerrak und Kattegat (vgl. ÖSTERGREN, 1909) für mit *C. lamarckii* identisch.

Hinzugefügt sei noch, dass LAMBERTS (1936) und Fräulein PAPENFUSS'

Annahme (1936), *C. lamarckii (palmstruchii)* und *C. capillata* seien an den Nematocysten zu unterscheiden, mindestens verfrüht ist, denn aus den Beobachtungen von Weill (1934) und Fräulein Papenfuss geht zwar hervor, dass *C. lamarckii* und *C. capillata* aus der Themsemündung und auch *C. palmstruchii* und *C. capillata* von Kristineberg (Schweden) in dieser Hinsicht Unterschiede aufweisen, es geht aber zugleich aus ihnen hervor, dass *C. capillata* von der Themsemündung und Kristineberg atriche Nematocysten von so verschiedener Grösse besitzen, dass man ebensogut diese beiden für verschiedene Arten halten kann. Offenbar ist die Variabilität in den Nematocysten der Lokalformen unter sich viel grösser als angenommen wurde; es wäre wichtig dies zu untersuchen.

Es sei schliesslich die Angabe Östergrens genannt, dass *C. palmstruchii* (= *lamarckii*) auf der menschlichen Haut beim Brennen keine Schmerz verursacht, während das Gegenteil für *C. capillata* gilt. Auch dies ist nie genauer untersucht worden [1]).

Untenstehende Liste enthält die Beobachtungen. Es sei nochmals darauf hingewiesen, dass sie zusammen mit der Tabelle 1 und der Karte (Fig. 1) benutzt werden muss. Weiter sei hinzugefügt, dass Fänge, die keine Quallen lieferten, nicht in dieser Liste genannt werden. Soweit sie auf Viertelstundfänge des Max Weber Beziehung haben, sind sie in der Tabelle 1 zu finden. Motorbootfänge, die keine Quallen lieferten, werden nirgends genannt, da ein negatives Resultat wegen der Kleinheit ihres Netzes wenig über das Nichtvorkommen von Quallen sagt. Man bekommt einen (zwar unvollständigen) Eindruck von der Anzahl der negativen Fänge (deren Wert im allgemeinen für die Beurteilung der Periodizität nicht gering ist) durch einen Vergleich der für die verschiedenen Arten genannten Daten: die Liste für *Cyanea* enthält 16 Daten vor dem 15. Juni 1934, dem frühesten Datum für *Chrysaora*.

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[1]) Von Interesse ist die Angabe Östergrens (1909), dass *C. palmstruchii* (= *lamarckii*), wenn sie als Meduse im Winter entsteht, farblos ist und dass die Tiere desto blauer sind, je später im Frühling sie entstehen. „Mitte Juni waren viele der grössten Exemplare ungefärbt, darunter das grösste, das ich überhaupt gesehen habe. Diese sind zweifellos im Winter entstanden und haben ihre Farblosigkeit bis zu ihrem Tode bewahrt. Diejenigen, die sich im Frühling oder im Vorsommer entwickeln, scheinen gefärbt zu werden, und zwar umso stärker, je weiterhin im Jahre sie entstehen. Diejenigen, die bis zur Mitte des Sommers leben bleiben, sind, auch bei einer Schirmbreite von nur 4–5 cm, stark gefärbt."

Es scheint mir ausgeschlossen, dass Östergren junge *C. capillata* für farblose *C. palmstruchii* hielt, denn er beschreibt auch *C. capillata* und diese Art tritt nach ihm später als *C. palmstruchii* auf, meistens nicht vor Mai (*C. palmstruchii* ab Januar).

LISTE DER BEOBACHTUNGEN

Cyanea lamarckii und *capillata*

27. II. 34. Zuidwal, 5.5–10 m, kleine Kurre: eine Qualle von 6.5 cm, gewiss *Cyanea*.

27. II. 34. Nieuwe Diep, kleine Kurre: eine Qualle, gewiss *Cyanea*.

10. III. 37. Zuidwal: 1 *Cyanea* von 6.5 cm angespühlt.

17. III. 35. Strand Huisduinen: 5 Stück von 7, 7.5, 7.5, 9 und 14 cm angespühlt.

27. III. 37. Marsdiep, Nordseite (von Heringnetzen gefangen): ungefähr 10 Stück von 6–8 cm.

2. V. 33. Zuiderhaaks, 8–11 m: 1 Stück von ± 20 cm.

6. V. 35. Nieuwe Diep: im Oberflächenplankton eine Anzahl Junge von einigen cm Durchmesser.

7. V. 33. Strand Huisduinen: einige angespühlt.

8. V. 34. Haaksgronden und Marsdiep: Nr. 36–42 der Tabelle I.

21. V. 33. Strand Huisduinen: eine Anzahl kleinere und reife Ex. angespühlt.

25. V. 33. Nieuwe Diep und ausserhalb: ziemliche Zahl kleinere und reife im Oberflächenwasser.

28. V. 33. Boomkensdiep, Terschelling: grosse Zahl in Stromkabbelung, an der Oberfläche.

28. V. 34. Texelstroom: Nr. 43–44* Tabelle I.

30. V. 35. Schulpengat: Nr. 66 Tabelle I.

2. VI. 39. Schulpengat: Nr. 116 Tabelle I.

5. VI. 35. Texelstroom: 67–68 Tabelle I.

15. VI. 34. Nordsee querab Texel: 45–50.

16. VI. 33. Ausserhalb Molengat, 18–22.5 m: ungefähr 20 Quallen, grösstenteils *Cyanea*. Ausserhalb Noorderhaaks, 16–17 m: grosse Anzahl Quallen, vor allem *Cyanea*.

17. VI. 38. Texelstroom: (89)–96.

18. VI. 35. Malzwin und Marsdiep: 69–72.

18. VI. 36. Marsdiep, Haaksgronden: 73–77.

23. VI. 38. Haaksgronden: 97–104.

25. VI. 34. Nieuwe Diep, kleine Kurre: Fang I: 13, Fang II: ± 42 Stück.

26. VI. 33. Zuidwal, kleine Kurre: Fang I (10–11 m): einige, Fang II (4–10 m): einige.

27. VI. 39. Malzwin, Vlieter, Texelstroom-Nord: 117*–122*.

10. VII. 36. Nieuwe Diep, kleine Kurre: 18 Stück.

21. VII. 33. Haaksgronden: 1–4.

28. VII. 33. Texelstroom: 5–8.

31. VII. 39. Schuitengat, Terschelling: 123–125.

1. VIII. 39. Schuitengat, Terschelling: 126*–127*.

13. VIII. 33. Zuidwal, kleine Kurre, 5–9 m: einige.

24. VIII. 33. Texelstroom: 9–14.

31. VIII. 37. Inschot (Wattenmeer): 86.

18. IX. 32. Zuidwal, kleine Kurre: einige.

26. IX. 34. Texelstroom: 54–56.

7. X. 32. Zuidwal, kleine Kurre: 1 Stück.

9. X. 32. Strand Callantsoog: 1 Ex. angespühlt.

Aurellia aurita

17. IV. 34. Haaksgronden: 30–35.

28. IV. 36. Nieuwe Diep: einige im Oberflächenwasser.

29. IV. 36. Nieuwe Diep: kurz nach Hochwasser sehr zahlreich im Oberflächenwasser, Grösse von 100 gesammelten Ex. 20 à 25 bis unter 6 cm.

5. V. 35. Nieuwe Diep: eine Anzahl ziemlich grosse an der Oberfläche.
6. V. 35. Nieuwe Diep: wie am 5. V. 35, Grösse 10–20 cm.
7. V. 33. Huisduinen-Falga: einige, mit reifen Gonaden, angespühlt gefunden.
8. V. 34. Haaksgronden und Marsdiep: 36–42.
21. V. 33. Huisduinen: eine Anzahl reife angespühlt.
25. V. 33. Nieuwe Diep und ausserhalb: ziemliche Zahl reife im Oberflächenwasser.
28. V. 33. Boomkensdiep, Terschelling: grosse Zahl in Stromkabbelung, an der Oberfläche.
30. V. 35. Schulpengat: Nr. 66.
2. VI. 39. Schulpengat: Nr. 116.
5. VI. 35. Texelstroom: 67–68.
15. VI. 34. Nordsee querab Texel: 45–50.
16. VI. 33. Ausserhalb Molengat, 18–22.5 m, und ausserhalb Noorderhaaks, 16–17 m: einige.
17. VI. 37. Texelstroom, Scheurrak: 78–83.
17. VI. 38. Texelstroom: (89)–96.
18. VI. 35. Malzwin und Marsdiep: 69–72.
18. VI. 36. Marsdiep, Haaksgronden: 73–77.
23. VI. 38. Haaksgronden: 97-104.
25. VI. 34. Nieuwe Diep, kleine Kurre: Fang I ± 509, Fang II ± 640 Stück.
26. VI. 33. Zuidwal, kleine Kurre: Fang I (10–11 m): einige, Fang II (4–10 m): einige.
27. VI. 39. Malzwin, Vlieter, Texelstroom-Nord: 117*–122*.
10. VII. 36. Nieuwe Diep, kleine Kurre: 3 Stück.
21. VII. 33. Haaksgronden: Nr. 1–4.
28. VII. 33. Texelstroom: 5–8.
31. VII. 39. Schuitengat (Terschelling): 123–125.
1. VIII. 39. Schuitengat (Terschelling): 126*–127*.
24. VIII. 33. Texelstroom: 9–14.

Chrysaora hysoscella

15. VI. 34. Nordsee querab Texel: Nr. 45–50.
17. VI. 37. Texelstroom, Scheurrak: 78–83.
17. VI. 38. Texelstroom: (89)–96.
23. VI. 38. Haaksgronden: 97–104.
27. VI. 39. Malzwin, Vlieter, Texelstroom-Nord: 117*–122*.
2. und 3. VII. 32. Nieuwe Diep: einige im Oberflächenwasser gesehen.
5. VII. 32. Nieuwe Diep: in grösserer Zahl im Oberflächenwasser. Sehr warmes Wetter.
7. VII. 32. Nieuwe Diep: zahlreich im Oberflächenwasser.
10. VII. 36. Nieuwe Diep, kleine Kurre: 3 Stück.
21. VII. 33. Haaksgronden: Nr. 1–4.
28. VII. 33. Texelstroom: 5–8.
31. VII. 32 und nächstfolgende Tage: Nieuwe Diep: jedesmal eine kleine Anzahl vielen *Rhizostoma* gegenüber.
31. VII. 39. Schuitengat (Terschelling): 123–125.
1. VIII. 39. Schuitengat (Terschelling): 126*–127*.
4. VIII. 32. Nieuwe Diep: kleine Zahl im Oberflächenwasser.
15. VIII. 33. Nieuwe Diep: ziemlich viele im Oberflächenwasser.
24. VIII. 33. Texelstroom: 9–14.
30. VIII. 33. Ausserhalb Noorderhaaks: Nr. 15.
4. und 5. IX. 35. Nieuwe Diep: sehr viele kleine im Oberflächenwasser.
13. IX. 32. Zuidwal, kleine Kurre, 2–8 m: 1 Ex.
18. IX. 32. Zuidwal, kleine Kurre: einige.
26. IX. 34. Texelstroom: 54–56 (alles kleine Tiere).
27. IX. 33. Haaksgronden: 16–19.

2. X. 32. Strand Callantsoog: einige kleine angespühlt.
7. X. 32. Zuidwal, kleine Kurre: 1 kleines Ex.
9. X. 32. Strand Callantsoog: einige kleine angespühlt.
16. X. 32. Strand Callantsoog: 4–6 ziemlich kleine angespühlt.
24. XI. 33. Fundort?: 2 von ± 15 und ± 5 cm.

Rhizostoma pulmo

17. VI. 37. Texelstroom, Scheurrak: Nr. 78–83.
27. VI. 39. Malzwin, Vlieter, Texelstroom-Nord: 117*–122*.
2.–3. VII. 32. Nieuwediep: einige im Oberflächenwasser.
10. VII. 36. Nieuwediep, kleine Kurre: 3 Stück.
21. VII. 33. Haaksgronden: Nr. 1–4.
28. VII. 33. Texelstroom: 5–8.
31. VII. 32 und nächstfolgende Tage: Nieuwediep: viele im Oberflächenwasser.
31. VII. 39. Schuitengat, Terschelling: 123–125.
1. VIII. 39. Schuitengat, Terschelling: 126*–127*.
15. VIII. 33. Nordsee ausserhalb Texel: nachts während Stillwasser sehr viele grosse Stücke am Boden, diese verschwinden wenn das Wasser wieder strömt.
15. VIII. 33. Nieuwe Diep: sehr grosse Zahl (vor allem grosse, aber auch kleine) im Oberflächenwasser.
24. VIII. 33. Texelstroom: 9–14.
27. VIII. 38. Schuitengat (Terschelling): 105*–106*.
29. VIII. 38. Schuitengat, Meep (Terschelling): 107*–112*.
30. VIII. 38. Schuitengat (Terschelling): 113–115.
31. VIII. 37. Blauwe Slenk, Inschot, Zuidoostrak (Wattenmeer): (85)–88.
13. IX. 32. Zuidwal, kleine Kurre, 2–8, vor allem 3 m: mehr als ein Dutzend.
18. IX. 32. Zuidwal, kleine Kurre: einige.
27. IX. 33. Haaksgronden: 16–19.
28. IX. 34. Texelstroom: 57–65*.
2. X. 32. Strand Callantsoog: ziemliche Zahl angespühlt.
7. X. 32. Zuidwal, kleine Kurre: einige.
9. X. 32. Strand Callantsoog: ziemliche Zahl angespühlt, ± 40 auf einige km.
16. X. 32. Strand Callantsoog: ± 100 südlich, viel weniger nördlich von Callantsoog angespühlt (Strecke jedesmal 1 km).
23. X. 32. Marsdiep: ein halbes Dutzend in einer Fischreuse.
24. X. 33. Haaksgronden, grosse Kurre, 12–17 m: 1 Stück.
30. X. 32. Strand Callantsoog: 2 Stück angespühlt.

Fassen wir diese Ergebnisse kurz zusammen, so ergibt sich folgendes.

Die ersten *Cyaneas* (*lamarckii* oder *capillata*) wurden im Februar beobachtet: am 27. II. 1934 wurde eine Meduse von 6.5 cm am Zuidwal, eine andere im Nieuwe Diep mit der kleinen Kurre gefangen; es wurde nicht auf die Art geachtet, aber zweifellos (sieh weiter unten) lag hier *Cyanea* vor. Märzfunde gibt es nur wenige, die Zahl der frühen Tiere scheint nur klein zu sein;

Aprilfunde fehlen ganz. Die Tiere wurden regelmässig gefangen im Mai, Juni und Juli (viele von der zweiten Maihälfte an bis Ende Juli), einige im August, September und Oktober. Späte Exemplare wurden am 7. und 9. X. 1932 beobachtet. *Cyanea* zeigt eine lange Periode des Vorkommens: Februar bis Oktober, auch die Zeit zahlreicheren Auftretens ist eine ziemlich gedehnte. Es ist aber noch unmöglich anzugeben, ob die Periode vielleicht so lang ist weil sie zwei Arten umfasst, die unter sich Unterschiede aufweisen.

Aurellia aurita erscheint bei Den Helder offenbar um Mitte April: am 17. IV. 1934 in 6 Viertelstundfängen 1 Stück, am 28.–29. IV. 1936 viele, in allen Grössen zwischen 20–25 und weniger als 6 cm, im Nieuwe Diep. Viele bis sehr viele können im Mai und Juni anwesend sein. Ihre Anzahl ist klein im Juli und August, das letzte Exemplar ist vom 24. VIII. 1933. Die Meduse von *Aurellia aurita* zeigt eine kurze Periode des Vorkommens, sie ist sehr bald nach ihrem Erscheinen zahlreich und verschwindet kurz nach der Periode der grössten Häufigkeit.

Chrysaora hysoscella erscheint Mitte (wahrscheinlich 1. Hälfte) Juni: am 15. VI. 1934 in 5 Viertelstundfängen querab Texel 4 Stück, am 17. VI. '37 in 5 Fängen an der Ostseite Texels 1 Stück. Schon in der zweiten Junihälfte dürfte diese prachtvolle Qualle in grösserer Zahl vorkommen. Eine Zeit des maximalen Auftretens kann eigentlich nicht angegeben werden, sie kommt vom Juni bis Ende September offenbar immer in geringer Anzahl vor. Die Oktober-Funde sind alle von 1932, das späteste Datum ist der 24. XI. 1933.

Rhizostoma pulmo schliesslich kommt bei Den Helder ab Mitte Juni oder Anfang Juli zur Beobachtung. Das früheste Datum ist der 17. VI. 1937, wenn an der Ostseite Texels 2 Stück in 5 Fängen zur Beobachtung kommen. Demgegenüber ergeben der 17. VI. 1938 in 5 und der 23. VI. 1938 in 6 Fängen kein einziges Exemplar, die Art kommt also wahrscheinlich nicht jedes Jahr so früh. Sie kann im Juli ziemlich allgemein sein, ihr Maximum fällt indessen wahrscheinlich später, die betreffenden Daten sind aber zu unvollständig. Die letzten Tiere wurden Ende Oktober notiert: am 30. X. 1932.

Es sei nochmals hervorgehoben, dass die Wahrnehmungen viel zu unvollständig sind um genaue Angaben über die Periodizität der behandelten Arten zu ermöglichen.

III. DIE PERIODIZITÄT UND IHRE URSACHEN

Eine Zusammenfassung der wichtigsten in diesem Kapitel gegebenen Tatsachen findet sich in englischer Sprache am Schluss (p. 425). Sie enthält zu gleicher Zeit die allgemeinen Folgerungen. Diese Zusammenfassung zu lesen ist zum richtigen Begriff der Tatsachen nötig und es hat für den Leser sogar Vorteile mit ihr anzufangen.

Die Tatsachen selbst sind bei jeder der behandelten Arten ungefähr wie folgt eingeteilt: 1. die Periode des Vorkommens der Ephyren und Medusen an der holländischen Küste, 2. die Periode des Auftretens in Westeuropa (von Südengland bis in die Ostsee und bis Norwegen), 3. die Verspätung der Periodizität nordwärts, 4. der Temperatureinfluss auf die Periodizität, 5. das Vorkommen der Medusen vor ihrem ersten Erscheinen und der Einfluss äusserer Faktoren auf letzteres, 6. der Einfluss solcher Faktoren auf die Anzahl der Medusen in verschiedenen Jahren.

1. *Cyanea lamarckii* Péron & Lésueur

Aus den obigen Wahrnehmungen geht hervor, dass die Medusen von *Cyanea* in den Jahren 33 bis 39 bei Den Helder gefunden wurden vom Februar bis in den Oktober und dass sie eine lange Zeit zahlreichen Auftretens in den Monaten Mai bis Juli zeigten. Dies stimmt gut zu den viel ausführlicheren Beobachtungen VAN DER MAADENS (1942 b), nach denen die Tiere frühestens im Februar, spätestens Anfang Oktober gefunden werden und vom Mai bis in den Juli (sogar bis in den August hinein) zahlreich sein können. Daraus lässt sich mit ziemlicher Sicherheit schliessen, dass *Cyanea* ausserhalb dieser Periode, also in den Monaten November, Dezember und Januar, nicht oder jedenfalls sehr selten als Meduse bei uns vorkommt.

Aus VAN DER MAADENS Beobachtungen gehr weiter hervor, dass *Cyanea lamarckii* vorkommt vom Februar bis in die zweite Septemberhälfte (praktisch nur bis Mitte August), *C. capillata* von Ende Mai bis in den Oktober hinein. Da *C. capillata* an der holländischen Küste soviel weniger allgemein als *C. lamarckii* ist, lässt sich noch nicht mit Sicherheit angeben, ob sie wirklich nur von Ende Mai bis in den Oktober vorkommt, sicher ist aber, dass die Periode des Auftretens der *Cyanea* nicht deshalb lang ist, weil wir mit zwei Arten mit verschiedenen Perioden zu tun haben, sondern allein schon der langen Periode des Auftretens der *Cyanea lamarckii* wegen.

Nach M. J. Delaps Beobachtungen (1905) bei Valencia (SW Irland) erreichten Ephyren von *C. lamarckii* von 4 mm Durchschnitt, die am 12.-18. März abgeschnürt wurden, am 5. April 7 mm, am 15. April 10, am 30. April 20, am 6. Mai 30 mm. Eine andere Meduse mass 50 mm am 29. Mai und ungefähr 80 mm am 10. Juni. Die Temperatur war bei diesen Versuchen 10–15° C. Aus diesen Wahrnehmungen lässt sich schliessen, dass in einem Monat eine Grösse von wenigstens 10, nach zwei Monaten von 50, nach drei Monaten von 150 mm erreicht werden kann. Somit wäre eine *Cyanea* von 15 cm wenigstens drei, ein Tier von 28 cm (sieh unten) sicher vier Monate alt. Aus Russells Beobachtungen (1931b) könnte man mit der nötigen Zurückhaltung schliessen, dass *C. lamarckii* draussen bei Plymouth zwischen Anfang April und Anfang Juni von ungefähr 2 bis ungefähr 15 cm an Grösse zunehmen kann. Die Wahrnehmungen der beiden Delaps bei Valencia draussen sind zu unvollständig dass sie als Basis für eine Schätzung der Wachstumsgeschwindigkeit dienen könnten. Man vergleiche aber auch was unten über das Wachstum der anderen Arten gesagt wird.

Medusen, die Ende Februar eine Grösse von ungefähr 6 cm haben, sind wahrscheinlich mindestens zwei Monate alt. Aus van der Maadens Beobachtungen geht hervor, dass kleine *C. lamarckii* bis Ende Juli vorkommen. Solche Tiere mögen ein bis zwei Monate alt und also im Juni geboren sein. Das bedeutet, dass die Ephyren wahrscheinlich vom Dezember bis spätestens in den Juni gebildet werden.

Fräulein Delap fand im Aquarium von Valencia (Irland) Strobilation im Januar und Februar and Anfang der Ephyrenabschnürung Anfang Februar und Mitte März. Draussen fand sie junge Tiere unter 4 cm Anfang Mai, grössere (5–12 cm) im Juni, grosse Tiere im August und September. Aus Brownes Angaben (1900) geht hervor, dass grosse Exemplare bei Valencia zahlreich sein können im August. Die Anwesenheit nur kleiner Tiere unter 4 cm Anfang Mai weist wohl auf Ephyrenabschnürung im März hin. Browne (1895) und Moore (1937) nennen für the Isle of Man nur *C. capillata*, keine *C. lamarckii*, die Angaben mögen sich aber auf *C. lamarckii* beziehen; es wird eine Ephyre noch für Ende April angegeben, junge Quallen wurden im Mai, grössere Anfang Juni bis August gefunden. – Bei Plymouth findet Russell (1931 b) *C. lamarckii* nur zwischen dem 9. April und 29. Juli. Die Tiere scheinen nicht sehr zahlreich zu sein, jedenfalls nicht jedes Jahr. Die April-Tiere sind grossenteils klein, 0.5–5 cm Diameter, im Laufe des Sommers nehmen sie allmählich an Grösse zu. Die grössten Exemplare erreichen etwas mehr als 15 cm, diese verschwinden Ende Juli. Aus seinen Angaben geht auch hervor, dass es kleine Tiere von nicht mehr als 1 cm bis Anfang und sogar Mitte Juni geben kann. Ephyren werden danach wahrscheinlich von Ende Februar bis Anfang Mai gebildet. Die Periode der Ephyrenbildung ist aber offenbar kürzer in Plymouth als an der holländischen Küste.

Genaue Angaben über das Auftreten bei Helgoland gibt es nicht, nach HARTLAUB (1896) sollte *C. lamarckii* da vorkommen vom Mai bis Mitte September, nach HAGMEIER (1930) gibt es laichreife Quallen in den Monaten Juni bis August. – KRAMP (1937) gibt an, dass *C. lamarckii* an "Skagens Nordstrand" zahlreich vorkommt im Juli und August. Er nimmt an, dass diese Tiere zum grössten Teil von der Jütischen Strömung aus dem südlichen Teil der Nordsee angeführt werden, ich komme darauf unten zurück, vergleiche Kapitel IV. – Gehen wir davon aus, dass ÖSTERGRENS Angaben über *C. palmstruchii* sich auf *C. lamarckii* beziehen (sieh oben), so erscheint die Art an der schwedischen Skagerrakküste im Januar; die Tiere sind dann sehr klein; sie erreichen nach ÖSTERGREN ihr Maximum im Juni und verschwinden meistens Mitte Juli, spätestens in der 1. Augusthälfte (den 11. VIII. 1908).

Aus diesen Angaben lässt sich schliessen, dass *C. lamarckii* in Valencia jedenfalls Ephyren liefert im März, in Plymouth von Ende Februar bis Anfang Mai, in Holland Dezember bis Juni, an der schwedischen Küste vom Dezember oder noch früher an. Daraus lässt sich folgern, dass die Ephyren viel früher (aber auch bis später) geboren werden an der holländischen und schwedischen Küste als in Südengland. – Die jungen Quallen zeigen sich in grösserer Zahl bei Plymouth und Valencia gleich nach der Geburt, vom April oder Mai an; in Holland ebenfalls vom Mai an, aber diese sind dann teils schon gross. – Die reifen Quallen findet man bei Irland Juni bis September, bei Plymouth im Juni und Juli (1926 waren sie im Juli schon verschwunden), in Holland Mai bis September (praktisch bis Juli oder August), bei Helgoland mindestens vom Juni bis in den September, bei Skagen wahrscheinlich vom Juli (Juni?) bis in den September, an der schwedischen Küste aber nicht nach Mitte Juli oder der 1. Augusthälfte. Es bestehen also Unterschiede für die verschiedenen Lokalitäten, es ist aber so ohne weiteres nicht deutlich, womit diese eventuell zusammenhängen.

Nach dem, was wir jetzt über Lichteinfluss auf periodische Erscheinungen wissen (vergl. besonders ROWAN, 1938), war ich anfangs geneigt anzunehmen, dass es die periodisch ändernde

Lichtmenge ist, die die Periodizität der Quallen beherrscht. Daneben könnte dann die Temperatur eine mehr oder weniger sekundäre Rolle spielen. Es sieht aber so aus, als ob dem nicht so ist und ein direkter Einfluss von der Temperatur auf die Periodizität ausgeht. Für *Cyanea* ist dies zwar nicht so leicht zu beweisen, für *Aurellia*, *Chrysaora* und *Rhizostoma* ist es aber wahrscheinlich, dass direkter Temperatureinfluss eine grosse Rolle spielt. Greife ich nun diesen Tatsachen vor und nehme ich für *Cyanea lamarckii* an, dass es die Temperatur ist, die die Ephyrenbildung (oder eigentlich die Strobilation) in Gang setzt, dann muss es eine niedrige Temperatur sein, die dies bewirkt, denn die Ephyren werden bei uns Dezember bis Juni und hauptsächlich Februar bis April [1]) gebildet. Die Minimum Wassertemperatur findet sich bei uns im Februar und März. Wenn aber eine so niedrige Temperatur, von vielleicht 4 bis 8° C, für die Ephyrenbildung günstig ist, so ist es begreiflich, wenn bei Plymouth die Periode der Ephyrenbildung kürzer dauert als in Holland, denn so niedrige Temperaturen werden da nur während kurzer Zeit im Frühjahr erreicht. Dieser Fall ist denn auch ganz dem von *Clupea harengus* L. und *Gadus merlangus* L. (und eventuell anderen Arten) bei Plymouth analog. FORD (1929, p. 18–22) findet da grosse Heringfänge, wenn die Temperatur in den Monaten November bis Februar niedrig, unter 12–11° C ist. Im Durchschnitt fällt die Temperatur aber nicht unter 11° vor der letzten Dekade des Dezember und die Monate November-Dezember solcher Jahre sind dann für die Heringfischerei ungünstig. RUSSELL (1935, p. 158–162) hat weiter nachgewiesen, dass der Wittling bei Plymouth sich fortpflanzt bei einer Temperatur zwischen 9 und 9.5° C. Er weist nun darauf hin, dass sie sich in der Nordsee (vgl. DAMAS, 1909, p. 39) bei 6–10° C fortpflanzt. "Off Plymouth the temperature rarely drops below 8° C and in some years does not drop below 9° C., so that evidently the period available for spawning is much more restricted than in more northern regions". Dies Alles besagt, dass wenigstens einer der obenerwähnten Unterschiede zwischen verschiedenen Lokalitäten, nämlich die kürzere Bildungsperiode der Ephyren bei Plymouth, erklärt werden kann und wir werden unten sehen, dass das auch für einen anderen Unterschied gilt.

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[1]) Die Hauptzeit für das Auftreten der Medusen fällt nämlich in die Monate Juni–Juli und die ältesten Medusen sind 4 Monate alt, die jüngeren zwei Monate.

Junge *Cyaneas* sind an der holländischen Küste im Monat Mai, wenn sie in grösserer Anzahl erscheinen – im Gegensatz zu dem was für die April-Tiere von Plymouth gilt – von sehr verschiedener Grösse und diese Tiere müssen also zu verschiedenen Zeiten als Ephyren abgeschnürt worden sein. Darauf weist auch das Vorkommen sehr junger Quallen bis ziemlich spät in den Sommer hinein hin; nach VAN DER MAADENS Beobachtungen findet man Tiere von nur 2 cm Diameter bis mindestens Ende Juli. Solche Tiere sind, wie wir sahen, nicht viel mehr als einen Monat alt und es müssen also Ephyren abgeschnürt werden vom Januar bis in den Juni hinein. Teilweise mag dieser grosse Unterschied in der Zeit der Ephyrenentstehung von Temperatureinflüssen herrühren, indem zum Beispiel eine zu hohe oder zu niedrige Temperatur die Abschnürung verlangsamt; so könnte in untiefem Wasser die Abschnürung zu einer anderen Zeit stattfinden als in tiefem. Daneben mag aber auch das Alter der Polypen eine Rolle spielen. Aus dem, was über das Vorkommen reifer *Cyaneas* bekannt ist (man findet sie von Ende Mai bis Ende August) und aus dem was wir für die nordamerikanischen *Cyaneas* wissen (BIGELOW, 1928, p. 357–358), geht hervor, dass auch die Fortpflanzungszeit der Medusen eine sehr gedehnte ist, so dass die Scyphistomas im Januar von sehr verschiedenem Alter sein müssen. Es ist nicht unwahrscheinlich, dass dies wiederum die Zeit der Strobilation beeinflusst. Weiter bleiben die Scyphistomas, wie wir durch Laboratorium- und Aquariumbeobachtungen wissen, mehrere (nach GRAEFFE viele) Jahre hintereinander am Leben und es ist nicht unmöglich, dass dabei auch zwischen Tieren verschiedener Jahrgänge Unterschiede in der Zeit der Ephyrenbildung bestehen; Fräulein DELAP beschreibt ein Scyphistoma, das in seinem ersten Frühling Ephyren zwischen dem 12. und 18. März, in seinem zweiten Frühling Anfang Februar gab [1]).

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[1]) HARGITT (1902 und 1910) beschreibt, wie Ephyren von *Cyanea* innerhalb 20 Tagen nach dem Festheften der Planula gebildet werden können. "The minimum time noted between the attachment of the planula and the assumption of the strobila stage was ten days, making the time from the origin of the planula to that of the strobila about seventeen days, or about eighteen to twenty days for the appearance of the ephyra" (1902, p. 558). "In the larger number the period was much greater than this, thirty to forty days under average aquarium conditions, while in some case there was no

Von Interesse ist, dass die Medusen im Ganzen nie vor dem Mai oder dem Juni zahlreich angetroffen werden, obgleich aus ihren Grössen hervorgeht, dass sie im März und April schon zahlreich sein müssen. Aus den Messungen VAN DER MAADENS (1942 b) geht hervor, dass *Cyanea lamarckii*, wenn sie Ende Mai zum ersten Mal zahlreich auftritt, eine Grösse von 1 bis 22 (sogar 28) cm hat. Die grösseren und grössten Tiere sind, wie wir sahen, vermutlich drei und vier Monate alt und also im Januar-Februar geboren. In der ganzen Periode zwischen dem Februar und Ende Mai sind sie aber höchst selten. In dieser Hinsicht nun sind die folgenden Bemerkungen von BIGELOW (1928, p. 358) für *C. arctica* (= *C. capillata*) von grossem Interesse. "Our failure to take them in our tow nets elsewhere in the Gulf during these months, in spite of the considerable number of hauls, recalls Louis Agassiz's remark (1862, p. 109) thar "there must be something peculiar in the habits of the young Cyanea to render them apparently so rare, when in the adult state they are so common" along the coasts of Massachusetts Bay. His suggestion that they keep near the bottom during their early stages has been corroborated by Mayer's observation (1910, p. 600) that young Cyaneas rarely come to the surface in the aquarium but spend most of their time clinging to the bottom or side of the tank with their widespread oral fringes. The tendency of the small Cyaneas to seek the surface so much more regularly about Woods Hole than in the Gulf of Maine is an interesting local difference in habits still awaiting explanation."

AGASSIZ (1862, p. 110–111) nahm an, dass *Cyanea* in ihrer Jugend in Bodennähe lebe, weil er selbst Aquariumbeobachtungen gemacht hatte, wie sie später von MAYER wiederholt wurden. "The youngest specimen of Cyanea versicolor seen by me was found swimming near shore, in the channel along Sullivan's Island, in Charleston harbor, and was kept for some time in confinement. It often suspended itself by the folds of the actinostome, to the sides of the glass vessel in which it was kept, and I am led to infer, from this circumstance, that this is a natural habit of the young *Cyaneae*, which may explain their rare appearance near the surface. The youngest specimen of Cyanea arctica, observed by my son, was in the habit of remaining attached to the bottom of the jar in which he kept it alive about ten days, hardly ever moving unless disturbed. We are so accustomed to consider Medusae as

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transformation even at the end of two months" (1910, p. 246). Diese kurze Dauer ist zweifellos für die Verhältnisse im Meer abnormal, obgleich es nicht ausgeschlossen zu sein braucht, dass sie auch da ab und zu vorkommt.

animals floating in the water and basking near its surface, that the explanation here given of the rare occurrence of young Cyaneae may appear questionable, and I would hardly have ventured to suggest it, had I not become acquainted with a kind of Medusa, in Florida, of which I shall give an account in another chapter, which is hardly ever seen at the surface of the water, at any time, even when adult, but found by thousands, groping in the mud and hardly moving, crowded upon one another, like barnacles upon rocks." Die von AGASSIZ gemeinte Meduse ist *Cassiopea frondosa* (Pall.).

MAYER hat also wahrscheinlich diese Gedanken AGASSIZ' übernommen, wenn er seine Aquariumbeobachtungen im Zusammenhang mit der Lebensweise der Medusen im Meere brachte. Nichtsdestoweniger bilden seine Beobachtungen (1910, p. 600) eine wertvolle Bestätigung der Wahrnehmungen AGASSIZ'. "When the young Medusa is about 7 mm. in diameter there are a number of slender papillae upon the exumbrella and these are clustered especially at the aboral apex. In this stage the medusa rarely comes to the surface, but frequently spreads its oral fringes out over the bottom or sides of the aquarium and remains sedentary. The same habit is exhibited by the closely allied "*Cyanea fulva*" which is represented in figs. 1 to 7, plate 66, and figs. 1 to 3, plate 67; and it is probably due to some such habit that the young are rarely to be found upon the surface while the large and mature medusae are very abundant." MAYERS plate 67, fig. 1, bildet ein solches Tier, das sich mit den Mundarmen festgesogen hat, ab.

Im Zusammenhang mit diesen Beobachtungen ist auch die folgende Angabe von Fräulein DELAP von Interesse. "*Cyanea* does not thrive in captivity as well as *Chrysaora*. It evidently requires more space than is given in an ordinary bell-jar of ten inches in diameter. It would remain for hours motionless on the bottom, and would not swim even to catch its food; but if a medusa was placed inside the frills, it quickly disappeared into the stomach." Es sei hinzugefügt, dass die jungen Medusen nach Fräulein DELAPS Wahrnehmungen eine grosse Vorliebe für kleine Hydromedusen als Nahrung haben.

Schliesslich seien die von HARGITT (1902, p. 558) an *Cyanea*-Ephyren von Woods Hole gemachten Beobachtungen genannt. "In habit the young ephyra appears somewhat sluggish, and, while capable of active movement by the contractions of its bell, lies rather quiescent in the aquarium, seldom moving except as stimulated by agitation of the water or otherwise. While in rest it lies upon the aboral surface, with the manubrium extended upward¹), probably a condition assumed for the capture of prey."

VAN DER MAADEN (1942 b) gibt nun an, dass *Cyanea* an heissen Tagen mit Südostwind schnell der Zahl nach zunimmt um mit Nordwestwind in grosser Anzahl angeschwemmt zu werden: „Das Meer wird gleichsam reingefegt". Die plötzliche Zunahme bei heissem Wetter könnte zwei Ursachen haben. Die erste ist, dass der Südostwind einen Bodenstrom nach der Küste verur-

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¹) Dieses am Boden liegen mit der Oberseite unten wird für die Ephyren der Rhizostomide *Mastigias papua* L. Agassiz beschrieben von UCHIDA (1926, p. 52).

sacht, der die Tiere in Landnähe bringt. Die zweite, dass das heisse Wetter sie an die Oberfläche bringt der grossen Lichtmenge oder der hohen Temperatur wegen. Da der Südostwind aber nicht im Stande ist die Tiere vor frühestens Mitte Mai in grösserer Anzahl an die Oberfläche zu bringen, so liegt die Annahme auf der Hand, dass die grosse Lichtmenge oder die hohe Temperatur dies verursachen. Das ist auch deshalb wahrscheinlich, weil das plötzlich späte Erscheinen offenbar von so weiter Verbreitung ist. Denn es wird nicht nur von BIGELOW für die Gulf of Maine, sondern auch von KRAMP (1937) für die dänischen Gewässer beschrieben. Da nun die Lichtmenge an heissen Tagen nicht plötzlich zunimmt und die Zunahme der Tiere eine ziemlich plötzliche ist, so liegt die Annahme auf der Hand, dass die hohe Temperatur die Tiere nach oben bringt. Ein Vergleich der *Cyanea*-Grafiken VAN DER MAADENS und Kurven der Meerwassertemperaturen für die Leuchtschiffe Noordhinder, Haaks und Terschellingerbank (Fig. 2) spricht nun dafür, dass plötzliche Temperaturerhöhungen zwischen 13° und 17° C (wahrscheinlich zwischen 14° und 17°, aber näher lässt sich die Sache nicht definieren) von grossem Einfluss sind. In der Nähe aller plötzlichen Temperaturerhöhungen in diesem Gebiet finden sich hohe *Cyanea*-Maxima. Die Erscheinung wäre aber erst durch mehr Beobachtungen zu beweisen.

Wenn wir nun in diesem Licht die obenerwähnten Beobachtungen über das Vorkommen der Medusen an verschiedenen Lokalitäten noch einmal durchsehen, so finden wir, dass die *Cyanea*s bei Plymouth, und zwar als kleine Tiere, schon im April oder Mai erscheinen, in Holland im Mai oder Juni, bei Helgoland vom Juni und bei Skagen vom Juni oder Juli an. Das weist also auf eine Verspätung nach dem Norden hin. Diese Verspätung wäre nun, wenn die Art überall in derselben Weise auf die Temperatur reagieren würde, leicht begreiflich. Sie findet sich nicht nur bei *C. lamarckii*; MAYER (1910, p. 599) und BIGELOW (1928, p. 358) beschreiben sie für *Cyanea arctica* (= *capillata*) in Nordamerika und wir werden ihr weiter unten bei *Aurellia* begegnen. Ausserdem finden wir sie für die Hydromedusen, von denen KRAMP (1927, p. 222) schreibt: "It is a general rule that medusae species in the warmest part of their area of distribution occur earlier in the year than in colder parts; various instances of this are noted in KRAMP & DAMAS (1925) in the case of Norwegian medusae, and also in my "Ingolf" papers." KRAMP nennt dann

einige Beispiele. – Nur die *C. palmstruchii* genannten Tiere von der schwedischen Küste passen nicht gut zu dieser Regel dass sie später als die südlicheren erscheinen, denn sie haben nach ÖSTERGREN ihr Maximum im Juni und verschwinden meistens Mitte Juli, spätestens in der 1. Augusthälfte, also eingentlich auffallend früh. Wenn das Alles richtig ist, so würde man, da auch hier die Medusen ab Januar anwesend sind, entweder annehmen müssen, dass die plötzliche Temperaturerhöhung, die günstig für das Heraufkommen der Medusen ist, besonderen Umständen zufolge an der schwedischen Küste früher statt später fällt als südlicher, oder dass die Tiere aus dem Skagerrak physiologisch etwas verschieden sind und auf niedrigere Erhöhungen reagieren. – Was den Süden von Grossbritannien betrifft, fällt es auf, dass die Periode später ist in Valencia Harbour, am offenen Ozean, als in Plymouth.

Aus VAN DER MAADENS Beobachtungen (1942 b) geht hervor, dass die *Cyanea*s das eine Jahr ziemlich viel früher als das andere verschwinden. Anfangs habe ich mir vergebens bemüht einen Zusammenhang zwisschen diesem Verschwinden der Medusen und der Temperatur in der Zeit dieses Verschwindens zu finden. Auch das Vorkommen anderer Arten (*Cyanea capillata*, *Aurellia aurita*) im Norden bis in den Winter hinein (sieh unten) weist nicht auf Temperatureinfluss beim Verschwinden hin. Es hat sich nun aber für *Aurellia*, *Chrysaora* und *Rhizostoma* herausgestellt, dass offenbar ein Zusammenhang besteht zwischen dem Verschwinden und der Temperatur in den Monaten der Ephyrenbildung oder Strobilation. Für *Cyanea* ist es mir nicht gelungen das Bestehen dieses Zusammenhangs festzustellen, wahrscheinlich weil der Unterschied im Verschwinden von Jahr zu Jahr nicht gross genug ist; ich nehme aber an, dass die Ursache auch für sie besteht. – In diesem Zusammenhang ist, wie sich bei der Behandlung der *Aurellia* zeigen wird, die folgende Beobachtung von Interesse, die uns auch aus anderem Grunde zu denken gibt. In der letzten Dekade des Juli 1936 gab es in Katwijk einen Tag von 14.000 *Cyanea*s per km, dann im weiteren Verlauf des Sommers fast keine mehr. Diese hohe Zahl war wahrscheinlich einer starken Temperaturerhöhung zuzuschreiben; die Wassertemperatur (Fig. 2) war bei Terschellingerbank im Durchschnitt 13° C in der zweiten, 15°.5 C in der dritten Dekade. Offenbar brachte also die plötzliche Temperaturerhöhung alle anwesenden Tiere an die Oberfläche, so dass es am Boden keine mehr gab. Aber wie konnten sich so viele Tiere zur gleichen Zeit am Boden vorfinden? Es wird sich bei der Behandlung der *Aurellia* zeigen, dass das hohe Maximum und das plötzliche Ablaufen der Medusenproduktion wahrscheinlich an erster Stelle dem Temperatureinfluss auf die Strobilation zuzuschreiben war. – Daneben ist die Beobachtung aus folgendem Grunde interessant. Man fragt sich nämlich, wo diese überzahlreichen *Cyanea*s denn bleiben? Wird das Meer wirklich bisweilen dermassen reingefegt, dass es keine Tiere mehr gibt? Oder ist die Lebensdauer der *Cyanea*s, nachdem sie einmal die Oberfläche erreicht haben, eine so beschränkte, dass in kurzer Zeit alle Tiere sterben? Letzteres kann ich fast nicht annehmen, aber unmöglich ist es nicht. Man findet nämlich nach VAN DER MAADENS Aufzeichnungen (1942 b) junge *Cyanea*s von einigen cm Diameter (also gut einen Monat alt) bis in die zweite Hälfte des Juli hinein. Kurz darauf sind die Tiere dann nahezu ganz oder ganz verschwunden. Da wir nun wissen, dass die Tiere im Frühling und Frühsommer mindestens drei bis vier Monate brauchen um ihre Maximumgrösse zu erreichen, so müssen diese späten Jungen verschwinden, ohne eine nennenswerte Grösse erreicht zu haben. Da nichts darauf hinweist, dass sie im Juli zum Bodenleben zurückkehren, müssen wir wohl annehmen, dass sie sterben. Da *C. lamarckii* schon bei sehr geringer Grösse geschlechtsreif werden kann, mag dieses Sterben dennoch von einem Sichfortpflanzen vorangegangen sein. Es wäre nun möglich, dass die Frühjahrstiere deshalb Zeit haben gross zu werden, weil sie sich nicht fortpflanzen bevor die Temperatur eine gewisse Höhe erreicht hat, während die Sommertiere keine Zeit zum Grosswerden haben, weil sie so früh reifen. Wenn beide Gruppen dann gleich oder kurz nach der Fortpflanzung sterben sollten, so wäre es begreiflich, dass man am Ende der Periode nur kleine Individuen sieht. Dieses könnte zugleich der Grund sein weshalb in der ersten Hälfte der Periode des Vorkommens die grossen Tiere sich relativ zahlreicher vorfinden und auch grösser sind als später, eine Tatsache auf die VAN DER MAADEN für verschiedene Arten hinweist.

Ich nehme an, dass die Fortpflanzung mit dem baldigen Sterben zu machen hat, obgleich die Angaben der HARGITTS (1910, p. 223) für *Cyanea arctica* (= *capillata*) auf das Gegenteil hinweisen könnten. Sie schreiben nämlich folgendes. "Following the liberation of the sexual products, and in the case of the females the final escape of the larvae, there seems to be a rather rapid decline in the vigor and activity of Aurelia and early death ensues. Many specimens may be found drifting along shore lines and in harbors, and, if there be wind or tide driving them shoreward, they become stranded and rapidly disintegrate. An examination of many such during the past summer showed that in most cases such specimens were dead or dying when they came ashore. The case of Cyanea seems somewhat different. This medusa seems to live for considerable time after passing the spawning period. As stated before, the breeding season is usually in spring. But it is not unusual to find many specimens during early and late summer swimming freely in the usual manner. It is, however, rare to find such specimens bearing genital products. In many specimens collected in Casco Bay during the past summer not one was found with gonads."

Bis so weit die Ursachen der Saisonperiodizität. Betrachten wir jetzt die Jahresunterschiede, so finden wir, dass die Zahl der *Cyanea*s offenbar sehr viel grösser war im Jahre 1935 als in den anderen Jahren, in denen VAN DER MAADEN Beobachtungen sammelte. Es ist genügend bekannt, wie stark das Heranwachsen von Jungtieren im Meer von Umwelteinflüssen abhängig ist und in wie starkem Masse zum Beispiel die praktische Fischerei von „guten", oder „schlechten" Hering- oder Schellfisch-Jahren beeinflusst wird. In vielen Fällen mag die Temperatur eine wichtige Rolle spielen, es bestehen aber verschiedene andere Ursachen, die RUSSELL (1935, p. 162–165) schon einmal resumiert hat. Obgleich ein einzelnes Beispiel vom Zusammengehen grosser Häufigkeit mit einem Umwelteinfluss natürlich nicht ausschlaggebend ist, sei darauf hingewiesen, dass die Dezember- bis Februar-Temperaturen in dem uns hier interessierenden Winter '34–'35 (Fig. 2) abnorm hoch waren, höher als in allen übrigen Jahren. Es ist also nicht unmöglich, dass warme Winter die *Cyanea*-Zahlen im nächsten Sommer günstig beeinflussen, wobei man allererst an die Günstigkeit einer etwas höheren Wintertemperatur auf die Ephyrenbildung denkt. – Es ist aber auch denkbar, dass die Häufigkeit der Medusen eine andere Ursache hat. Die Scyphopolypen können sich durch Knospenbildung stark vermehren. Wir wissen nicht was diese Knospenbildung beeinflusst, aber wenn unter besonderen Umständen jeder Polyp sich zehnfach vermehren würde, wäre auch die Zahl der Ephyren zehnfach vermehrt. Nun könnte auch die Knospenbildung unter Temperatureinfluss stehen und in bestimmten Wintern (sie findet besonders im Herbst oder Winter, vor der Strobilation, statt) stark begünstigt werden. Damit wäre aber auch Zunahme der Medusen auf diesem Wege auf Temperatureinfluss zurückgeführt. – Leider wissen wir von einem Einfluss von Milieufaktoren auf die Knospenbildung der *Cyanea*-Scyphistomas ebenso wenig wie von ihrem Einfluss auf die Ephyrenbildung. Ich habe nicht einmal Angaben darüber gefunden in wie weit Knospenbildung bei *C. lamarckii* eine Rolle spielt [1]).

Sogar über das Vorkommen der Scyphistomas an unserer Küste ist nichts bekannt und nicht viel besser steht es damit im übrigen Westeuropa. DAMAS (1909) nimmt für *C. capillata* an, sie werde ausschliesslich in unmittelbarer Nähe des Landes geboren. Obgleich dieses wohl zutrifft (vergleich auch die Auseinandersetzungen BIGELOWS), so ist es wahrscheinlich, dass die Scyphistomen nicht an untiefes Wasser gebunden sind, sondern bis relativ tief (70 m) vorkommen können (BIGELOW, 1928, p. 359).

2. *Cyanea capillata* (L.)

Wie schon erwähnt, deuten VAN DER MAADENS Beobachtungen darauf hin, dass *C. capillata* bei uns vorkommt von Ende Mai bis in den Oktober. Da *Cyanea* früh im Jahr so selten gefunden wird, braucht die Möglichkeit nicht ausgeschlossen zu sein, dass *C. capillata* früher erscheint. Obgleich die Zeit ihrer grössten Häufigkeit, wie die der *C. lamarckii*, in den Juni und Juli fällt, bekommt man den Eindruck, dass die Periode als ganzes, verglichen mit der der *C. lamarckii*, etwas später fällt; besonders das Vorkommen relativ vieler Tiere (± 30 auf 1 km) im September 1933 ist auffallend. Ausserdem werden wir weiter unten sehen, dass auch in den dänischen Gewässern *C. capillata* später als *C. lamarckii* auftritt, woraus wir folgern dürfen, dass dies auch für Holland gilt. Der Unterschied ist aber weniger ausgesprochen als aus STIASNYS Angaben (1930, p. 20, vergleiche auch VAN DER MAADEN 1942 a, p. 68) hervorgehen würde.

Aus Messungen VAN DER MAADENS (vergleiche seine Tabelle 1) geht hervor, dass die Medusen, wenn sie in der letzten Dekade des Mai erscheinen, ziemlich klein sind und erst allmählich einen grösseren Durchmesser erreichen. Die grössten sind bis 17 cm Ende Mai, 30–35 cm Mitte Juni oder später, was auf ein sehr schnelles Wachstum hindeuten würde, wenn dieser Schluss erlaubt wäre. Wir können mit ziemlicher Sicherheit behaupten, dass Tiere von 17 cm mindestens 6 Wochen und höchstens 3 Monate alt sind und sie würden also im März geboren sein.

Nach VAN DER MAADENS Messungen kommen kleine Tiere von 2–3 cm bis Mitte und sogar Ende Juli vor. Solche Tiere sind wohl nicht viel älter als einen Monat und Ephyren würden also noch im Juni abgeschnürt werden. Die Periode der Ephyrenbildung würde also die Monate März bis Juni umfassen.

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[1]) HARGITT (1902, p. 557, 1910, p. 248) sagt von *Cyanea arctica* (= *capillata*) bei Woods Hole, dass Stolonisation "is a much less common feature in Cyanea than in Aurelia, though not by any means rare".

Was das eventuelle Vorkommen der *C. capillata* in Westengland (Isle of Man) anbelangt, sei auf das unter *C. lamarckii* gesagte verwiesen. Nördlicher, an der Westküste von Südschottland (Firth of Clyde), wurde *C. capillata* nach BROWNE (1906, p. 775) viel gefunden im Juli und weiter im September und Oktober. Ein junges Tier von ungefähr 15 mm wurde noch am 5. September gefunden.

Nach HAGMEIER (1930) fällt die Laichzeit für *C. capillata* bei Helgoland vom August bis Anfang September; „das Festsetzen der Planulae scheint bisweilen erst nach längerem Umherschwimmen stattzufinden, bei einem Versuch wurden noch nach vier Wochen schwimmende Planulae angetroffen" [1]). Strobilation wird für den Dezember (1924) und den Februar (1928) erwähnt; diese Angaben beziehen sich auf Aquariumbeobachtungen. Die Quallen erreichten nach 70 Tagen 30, nach 3 Monaten 50 mm; es ist anzunehmen, dass dieses Wachstum nicht optimaler Umstände wegen zu langsam war. – Es bestehen für die schwedische Küste Angaben von AURIVILLIUS (1898 b, p. 8–9). Nach ihm treten junge Tiere Anfang Mai auf [2]). Sie erreichen ihre volle Grösse nach Mitte Juni und stammen vermutlich aus Ephyren, die Ende Februar bis Ende April gefunden wurden. Geschlechtsreife Tiere gibt es im Sommer und Herbst viele, im Januar sind sie schon seltener, in den Monaten Februar bis April kommt nur ein einzelnes Exemplar vor (so am 16. II. 1895, bei einer Wassertemperatur von + 1° C, ein Exemplar, dessen Eier sich in einigen Tagen zu Planulae entwickelten; ein anderes Ex. wurde am 7. III. bei einer Wassertemperatur von — 1° C gefunden). Da es auch Ephyren im Herbst (Ende September bis Oktober) gibt, nimmt AURIVILLIUS an, dass sie es sind, die die Wintertiere liefern, insoweit letztere nicht von anderswo ins Skagerrak hinein geführt werden. Die Schwierigkeit ist aber, dass er die Ephyren der *Aurellia* und *Cyanea capillata* nicht unterscheiden konnte, was die Sache etwas unsicher macht. – Auch nach ÖSTERGREN tritt *C. capillata* an der schwedischen Küste nicht vor dem Mai auf. Ihr Maximum erreicht die Art dort nach ihm in den Monaten August bis Oktober. Sie verschwindet, „bis auf einzelne Exemplare", im November und Dezember. Letztere Angabe bildet also eine Bestätigung der Angaben des Aurivillius. – Kramp (1937, p. 182) gibt an, dass die Strobilation in den dänischen Gewässern hauptsächlich im März und April stattfindet; in geringerem Masse kann sie aber auch im Laufe des Sommers stattfinden, mit einem neuen Maximum im Herbst. Worauf diese Beobachtungen fussen, weiss ich nicht. Auch Kramp weist, jetzt für diese Art, auf die lange Abwesenheit der Medusen im Frühling und im Zusammenhang damit auf das Verhalten der *Cyanea* im Aquarium hin [1]), vergleiche oben, Seite 383–384. Nach ihm sind die Tiere zahlreich im Juli und August, wonach sie an Zahl abnehmen. Eine Anzahl grosse Individuen „der Frühlingsgeneration" kann man indessen noch bis in den Winter hinein antreffen.

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[1]) HARGITT (1902) beschreibt ähnliches für *C. arctica* (= *capillata*) in Nordamerika.

[2]) In seinem anderen Beitrag spricht AURIVILLIUS über Anfang Juni.

In der Ostsee kommen die Ephyren von *C. capillata* nach Kramp später als an der schwedischen Küste vor.

Schliesslich fand M. Sars (1841) bei Bergen (Norwegen) am 13. April (1837) *Cyanea*-Medusen von ungefähr 12 mm, die er für *C. capillata* hielt, und er beschreibt Planulae, die er am 19. September und 12. Oktober (1839) aus Medusen der *C. capillata* von 15–20 cm Durchmesser erhielt. Nach Damas (1909, p. 101) erscheinen die Medusen der *C. capillata* früher "in the southern than in the arctic regions".

Fassen wir diese Angaben zusammen, so finden wir Ephyren in Holland von mindestens März bis Juni, an der schwedischen und dänischen Küste von Ende Februar bis Ende April, und nach Kramp den ganzen Sommer hindurch, mit einem neuen Maximum im Herbst, das mit dem von Aurivillius erwähnten Vorkommen von Ende September bis Ende Oktober übereinstimmen mag.

Die jungen Medusen finden wir in Holland ab Mai und die Tiere verschwinden frühestens im Juli, spätestens Anfang Oktober. An der schwedischen Küste erscheint *C. capillata* Anfang Mai oder Juni (vgl. oben), einige Tiere bleiben da während eines grossen Teiles des Winters am Leben.

Es sieht also aus, alsob die Zeit des Erscheinens der Ephyren und Medusen sich nach dem Norden hin nicht oder wenig verspätet, während die Periode des Vorkommens im Norden sich verlängert weil die Zeit des Verschwindens viel später als im

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[1]) Da es hier ein Handbuch gilt, wird die Literatur nicht angegeben, aber ich nehme an, dass Kramp hierbei auf Agassiz, Mayer oder Bigelow fusst, vergleiche unter *C. lamarckii*.

Süden fällt. Wie bei der Behandlung der *C. lamarckii* schon gesagt wurde, gilt die Verspätung der ganzen Periode auch für *C. capillata* in Nordamerika.

Nicht nur Aurivillius, Östergren und Kramp nennen das Vorkommen einzelner *Cyanea capillata* bis in den Winter hinein, es wird von Mc Intosh (1927, p. 12) auch für die Küste von Schottland angegeben und genau wie nach Kramp in den dänischen Gewässern handelt es sich auch hier um grosse Stücke. "During mid-winter a huge Cyanea occasionally may be caught at a depth of 15 to 20 fathoms off the Bay – a solitary survivor of the swarms of summer." Und er fügt dann zu: "So far as the records go, the captures in December at St. Andrews appear to be more plentiful than at Plymouth, especially as regards the Coelenterates". Dieses späte Vorkommen nach dem Norden hin ist interessant in Anbetracht des späten Vorkommens im Norden einer Anzahl anderer Tiere mit mehr oder weniger südlicher Verbreitung. Unter diesen gibt es verschiedene Arten von Fischen, die aus dem südlichen Teile der Nordsee im Winter ganz verschwinden, im Norden aber regelmässig in kleiner Anzahl vorkommen: *Zeus faber* L., *Caranx trachurus* L., *Galeus vulgaris* Flem., u.a., ich werde darauf in einem späteren Beitrag zurückkommen. Es unterliegt meiner Meinung nach keinem Zweifel, dass sich diese Tiere deshalb so spät im Norden vorfinden, weil da die Temperaturen noch spät im Jahr relativ hoch sind wegen der grösseren Tiefe und somit grösseren Wärme des Wassers in dem nördlichen Teile der Nordsee dem südlichen gegenüber. Unwillkürlich fragt man sich, ob dies auch für die Medusen gelten könnte. Und da kommen wir zu dem Schluss, dass dem gewiss nicht so ist, denn wir werden unten, für *Aurellia*, finden, dass sie im Winter im Norden bei so grosser Kälte vorkommt, dass sie einfach einfrieren kann. Das späte Vorkommen der Quallen im Norden ist denn auch gewiss nur die notwendige Folge der allgemeinen Verspätung in der Zeit des Vorkommens nach dem Norden hin, es ist nur Folge des späten Endens der Strobilationsperiode. Die ganze Periode fällt da später, sie endet also auch später. Das würde zugleicherzeit besagen, dass die spät im Winter gefundenen Tiere aus spät im Herbst gefundenen Ephyren stammen, wie Aurivillius schon annahm. Sie würden also nicht zur "Frühling-Generation" gehören, wie Kramp glaubte.

Wenn es richtig ist, dass die Periode der Ephyrenbildung in Holland März bis Juni, in den dänischen und schwedischen Gewässern März bis Ende Oktober dauert, so liegt die Annahme auf der Hand, dass wir hier einen ähnlichen Fall vor uns haben, wie wir denselben schon unter *C. lamarckii* antrafen. Da fanden wir eine kurze Fortpflanzungsperiode bei Plymouth, weil die Temperatur im Winter erst sehr spät genügend niedrig wurde. Ähnliches könnte nun für *C. capillata* gelten: vielleicht wegen der hohen Temperatur im südlichen Teile der Nordsee im Sommer endet die Strobilation dort früh, während sie im Norden länger fortdauern kann. Die zeitweise Unterbrechung der Ephyrenbildung im Sommer an der schwedischen Küste könnte dann in der gleichen Tatsache, in einer zu hohen Sommertemperatur, ihre Ursache haben.

Die jungen *Cyanea capillata* sind, wenn sie sich Ende Mai zum ersten Mal zeigen, wie oben schon zur Sprache kam, höchstens 15–20 cm gross. Diese grössten Tiere mögen 2–3 Monate (oder, wenn sie sehr schnell wachsen sollten, 6–10 Wochen) alt sein und sie haben also, genau wie die jungen *C. lamarckii*, eine gewisse Periode ihres Lebens in Bodennähe verbracht. Diese Periode ist wahrscheinlich nicht viel kürzer als die der *C. lamarckii*, denn die Ephyren werden zwar später als bei dieser Art geboren, die jungen Quallen erscheinen aber durchschnittlich wahrscheinlich auch später als bei ihr. Wir hörten schon, dass KRAMP (1937) das „Bodenleben" auch für die dänischen Gewässer erwähnt und dass es auch bei *C. arctica* in Nordamerika gefunden wird, die mit *C. capillata* identisch oder ihr sehr nahe verwandt ist.

Die Zahl der von VAN DER MAADEN gefundenen *C. capillata* ist zu klein um feststellen zu können, was das Erscheinen der Medusen ab Ende Mai verursacht. Vermutlich spielt auch hier die Temperatur eine wichtige Rolle, aber gerade in Anbetracht der nahen Verwandtschaft der beiden Arten und anderseits der Unterschiede in ihrer Biologie wäre es von grossem Interesse eben dies mit Sicherheit festzustellen. Der Hauptunterschied im Vorkommen der beiden Arten ist der, dass die Strobilation der *C.lamarckii* im Dezember und Januar anfängt, während die Medusen spätestens im September verschwinden, dass die Strobilation der *C. capillata* Ende Februar oder im März anfängt, während die Medusen bis spät in den Winter hinein verschwinden. Bei *C. lamarckii* ist die Periode der Ephyrenbildung, bei *C. capillata* die des Vorkommens der Medusen teilweise auf den Winter verlegt. Es bestehen also vermutlich grundlegende Unterschiede in der Reaktion beider Arten äusseren Einflüssen gegenüber. Wie gesagt, ist

VAN DER MAADENS Material aber zu klein, hier einen eventuellen Temperatureinfluss nachzuweisen. Einmal scheint Übereinstimmung im Anschwimmen mit *C. lamarckii*, dann wieder mit *Aurellia aurita* (sieh unten) zu bestehen, so dass ein brauchbarer Hinweis fehlt.

Über eventuelle Unterschiede im Verschwinden der *C. capillata* in verschiedenen Jahren lässt sich an der Hand von VAN DER MAADENS Material nichts sagen. Nur 1933 kamen die Tiere offenbar bis später in den Sommer (September) vor. Diese Septembertiere massen 13–20 cm und dürften Anfang bis Mitte Juli geboren sein. Der Juli 1933 war nicht kalt, sondern warm. Die Annahme liegt also sicher nicht auf der Hand, dass die Tiere sich lange fortpflanzten, weil die Temperatur lange niedrig blieb.

Es sieht aus alsob *C. capillata* am zahlreichsten war in den Jahren, in denen auch *C. lamarckii* zahlreich auftrat. Das würde bedeuten, dass warme Winter an der holländischen Küste für beide Arten günstig sind. Sicherheit darüber besteht aber keineswegs.

3. *Aurellia aurita* (L.)

Aurellia aurita kommt bei Den Helder frühestens um die Mitte des April zur Beobachtung und 1934 war sie am 8. Mai schon sehr zahlreich. VAN DER MAADEN hat keine Funde vor dem Mai und keine Maxima vor Mitte Mai. Der Unterschied mag teilweise daran liegen, dass die frühen Beobachtungen bei Den Helder resp. am 17. IV. und 8. V. 1934 sich auf in Bodennähe lebende Tiere beziehen. Teilweise mag aber ein geringer Unterschied im Auftreten zwischen Katwijk und Den Helder bestehen, der vielleicht auf die eventuell grössere Häufigkeit von *Aurellia* in Brackwassergebieten zurückzuführen ist, sieh unten. Die Ohrenqualle ist nämlich (vergleiche besonders BIGELOW, 1928, p. 362–363) eine typische Form des mehr oder weniger brackigen Wassers, sie ist am zahlreichsten in den Mündungsgebieten der Flüsse, reicht zum Beispiel in der Ostsee bis an die finnische Küste heran, wo die Salinität nur ungefähr $6^0/_{00}$ beträgt. – VAN DER MAADENS Beobachtungen zeigen, dass die Zeit des Maximalauftretens in Katwijk zwischen halb Mai und spätestens halb Juli liegt. Die Meduse ist also sehr bald nach ihrem ersten Erscheinen zahlreich. Die Art verschwindet zwischen Mitte Juli und Ende August, VAN DER MAADEN fand in den Jahren 1933 und '35 noch eins resp. einige im September, das letzte am 28. dieses Monats. Im allgemeinen ist die Periode des Vorkommens der *Aurellia* an der holländischen Küste viel weniger gedehnt als die der *Cyaneas*, nach VAN DER MAADENS Diagrammen wurde 1934 das erste Exemplar am 11. Mai, das letzte am 13. Juli gesehen; 1935 ergab aber nach diesen Beobachtungen eine viel gedehntere Periode, vom 2. April bis zum 28. September.

Die früh erscheinenden Tiere sind von sehr verschiedener Grösse: 5 bis 20 (vielleicht bis 25) cm Ende April und Anfang Mai. Die grössten Tiere von VAN DER MAADEN massen 29 und 34 cm in der letzten Dekade des Mai. Tiere von 20 und mehr cm sind mindestens 3 Monate alt und die genannten sind also spätestens im Februar geboren. VAN DER MAADEN fand kleine Tiere von 4–6 cm noch im August. Solche Tiere sind höchstens zwei Monate alt und also im Juni geboren. Die Entstehungsperiode für *Aurellia* sollte an der holländischen Küste also Februar bis Juni sein. Meistens endet die Periode aber früher.

Nach Fräulein M. J. DELAPS Beobachtungen (1907) in Valencia Harbour (Irland) wachsen die Ephyren in ungefähr einem Monat von 4 bis mindestens 10 mm heran. Weiter erreichte eine *Aurellia*, die am 5. Juli 35 mm mass, am 10. Juli 45, am 15. Juli 60 mm; eine andere wuchs von 50 bis 70 mm zwischen dem 8. und 16. Juni. Fräulein DELAP legt den Nachdruck auf den grossen Einfluss genügender Nahrungsmengen. Die Angaben beziehen sich auf Tiere in Gefangenschaft.

Nach den Wahrnehmungen von M. SARS (1841) in der Nähe von Bergen (Norwegen) wuchsen Tiere im Meere zwischen dem 22. März und dem 11.–20. April von ungefähr 6 bis 25 mm heran.

HAGMEIER (1930, p. 559) sagt: „Im Alter von etwa drei Wochen entwickeln sich die Tentakel bei einem Durchmesser von 9 bis 10 mm (DELAP, 1907, l.c. und Helgoland). Im Alter von etwa fünf Wochen wachsen die Mundarme aus und das Tier enthält die halbkugelige Gestalt der *Aurelia* (Durchmesser etwa 13 mm)." Diese Angaben beziehen sich auf Aquariumbeobachtungen. HAGMEIERS Angabe, nach welcher die Quallen in etwa 7 Monaten einen Durchmesser von 100 mm erreichten und dann geschlechtsreif wurden, besagt dass diese Tiere viel zu langsam wuchsen.

AURIVILLIUS (1898 b, p. 8–9) nennt für Tiere an der schwedischen Küste eine Grösse von bis 25 mm am 8. und 11. Mai (1895), von 90 mm am 28. Mai, von 140 mm am 15. Juni. Die Wassertemperatur am 8.–11. Mai war dabei 12°.5.

Auch USSING (1927) gibt Masse für Tiere im Meer. Nach seinen Beobachtungen im Mariagerfjord (Ostjütland, Dänemark, Salinität 14–15$^0/_{00}$) erreichten Tiere, die am 27. Mai (1923) 12–15 mm massen, am 8. Juli bis 65 mm.

LOHMANN (1908) findet bei Kiel kleine Medusen von 1–2 cm Durchmesser von Anfang Mai an. Mitte Juni erreichten "die mit dem Netz gefangenen Aurelien" 10 cm Durchmesser, Ende Juni fand er solche von 20 cm, Ende Juli Schwärme grosser ausgewachsener Tiere, deren Grösse aber nicht angegeben wird.

Schliesslich gibt Wikström (1921) Masse (in mm) für die Tiere in den Schären SW. Finnlands, in 6.5–5.5$^0/_{00}$ Salzgehalt (Wikström 1936):

	Klein	Mittelgross	Grösste
Anfang Juli	5—8	9—12	17
Ende Juli	13—17	26	37
Mitte August	13—17	20—26	60

1932 fügt er dann noch andere Angaben hinzu: im Juni erreichen die Tiere eine Mittelgrösse von etwa 10 mm, aber unter günstigen Verhältnissen können Ende Juni Quallen von 35–40 mm als Seltenheit vorkommen; im Juli ist die Mittelgrösse etwa 20–30 mm, es gibt daneben spärlich Tiere von 50–60 mm; im August ist die Mittelgrösse etwa 60–70 mm. Viel grösser als 70 scheinen die Tiere da nicht zu werden.

Nach diesen Wahrnehmungen wachsen *Aurellia*s im südlichen Teile der Nordsee wahrscheinlich in ihrem ersten Monat bis mindestens 15 mm heran, im zweiten Monat bis sicher 40 oder 50 mm. Es scheint, dass bei Anwesenheit genügender Nahrung die Tiere innerhalb drei Monaten bis über 20 cm erreichen können. Danach wären die grösseren Medusen, die Anfang Mai bei uns erscheinen, im Februar-März als Ephyren abgeschnürt worden. – In der Adria soll *Aurellia* etwas langsamer wachsen, denn Graeffe (1884, p. 343) sagt, dass die im Oktober gelösten Ephyren in circa vier Monaten zu geschlechtsreifen Medusen heranwachsen". Diese Angabe fusst auf Wahrnehmungen im Meer.

Über die Periodizität der Aurellien finden sich viele Angaben in der Literatur. Ich behandle die Ephyren und Medusen gesondert und fange mit den Ephyren an.

Browne (1900) erwähnt für Valencia Harbour, Irland, Funde von Ephyren für den 14. Februar 1896, den 14. Januar und im Februar 1897, Februar und März 1898. "The scarceness of the Ephyrae during the spring seems to indicate that the Scyphistoma stage is either absent or very scarce in the harbour." In Fräulein Delaps Züchtungsversuchen kamen die ersten Ephyren am 28. Dezember (1903), 13. Februar (1904) und 4. April (1903) frei. Die Unterschiede in der Zeit zwischen verschiedenen Scyphistomen waren sehr gross. Im Jahre 1904 wurde die oberste Ephyre der frühesten Scyphistomen am 13. Februar abgeschnürt, während andere Polypen ihre ersten Ephyren erst im Laufe des Monats März abgaben. Ausserdem mag eine Periode von einer Woche zwischen der Abschnürung der ersten und letzten Ephyren einer Scyphistoma liegen, denn Fräulein Delap (1905) beschreibt für *Cyanea lamarckii* die Abschnürung von 12 Ephyren zwischen dem 12. und 18. März. Die 1900–1901 Temperaturen des Aquariumwassers waren (M. J. Delap, 1905) im Dezember 11–13, Februar 7–11, März 8.5–12, April 9.5–14°; 11° C ist all diesen Monaten gemeinsam. Im Meer wurden Ephyren gefunden am 14. und 20. Februar und am 5., 16. und 30. März (Jahre 1899–1901). – In Marine Fauna of the Isle of Man (MOORE, 1937, p. 52) werden Ephyren für die "hatching ponds" in Port Erin für den Januar und Februar jedes Jahres, für das Aquarium für den März (1900) angegeben. BROWNE (1895, p. 412) nennt sie für Ende März und Anfang April (1894). – In der Firth of Clyde an der Westküste von Südschottland wurden Ephyren im Jahre 1902 zwischen dem 25. Februar und dem 3. April gesehen (insgesamt nur 5 Stück) (BROWNE, 1906, p. 775). – Für Plymouth wird in Plymouth Marine Fauna (p. 85) angegeben: "The ephyrae appear in Febr. and may be taken in shoals during the first fortnight of Mar., they metamorphose towards the end of the month and begin to disappear". Für das Aquarium werden Ephyren (bisweilen Tausende) für die Zeit zwischen Ende Januar und Ende März angegeben.

„Auf Helgoland beginnt die Entwicklung der Strobila meistens in der zweiten Dezemberhälfte und zieht sich bis in den März hinein" (HAGMEIER, 1930, p. 554). Es betrifft hier Aquariumbeobachtungen. Die genaue Zeit der Ephyrenabschnürung wird nicht angegeben. Nach THILL (1937, p. 92) sollten die Ephyren bei Helgoland draussen im Dezember-Januar gefunden werden. Die Angabe scheint auf eine Mitteilung WULFFS zu fussen, nach der die jungen Medusen sich da Januar bis Mai finden sollten, eine Mitteilung die wohl unrichtig ist, sieh unten. – USSING (1927) gibt für Mariagerfjord (Ostjütland) Strobilation für Februar bis April, Ephyren für die Monate April bis Juni (1923) an. Ich denke, März bis Juni dürfte wohl richtiger sein. Im Aquarium kamen die ersten Ephyren am 4. April frei. – LOHMANN (1908) findet die Ephyren bei Kiel vom 30. I. an, regelmässig im Februar und im März, bis in die letzte Dekade des April, die Angabe scheint mir aber nicht vollkommen sicher [1]). BOGUCKI (1933) findet 1932–'33 die Ephyren bei Hel (Polen) in den Monaten Mai–Juni. Schliesslich geht aus WIKSTRÖMS Beobachtungen im Finnischen Meerbusen (1932) hervor, dass da die Zeit des

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[1]) Es ist nämlich nicht deutlich, ob er die Ephyren als zu *Aurellia* gehörig erkannte oder nur annahm, sie seien von der *Aurellia*. Er schreibt nämlich von den Quallen selbst: „Von Acraspeden Medusen kommt nur *Aurelia aurita* L. in Betracht; *Cyanea capillata* L. ist zu selten, um mit so kleinen Netzen noch gefangen zu werden". Nach der Behandlung der Medusen geht er dann ohne weiteres auf die der Ephyren über.

Ephyrenvorkommens im Mai bis Juni liegt. Er fand zahlreiche Ephyren von 2–9 mm Grösse am 8. Juni 1921.

Zuletzt seien M. SARS' Wahrnehmungen in der Nähe von Bergen (Norwegen) erwähnt. Aus seiner Beschreibung geht hervor, dass er am 22.–23. März (1837) eine Menge kleiner Medusen von 6–12 mm fand, die am 11.–20. April ungefähr 25 mm erreicht hatten. Zugleicherzeit fand er am 11. April nicht wenige, deren Entwicklung nicht weiter als die der Märztiere vorgeschritten war. Hieraus lässt sich schliessen, dass die Ephyren jedenfalls im März abgeschnürt werden. Es ist sehr interessant, dass für die norwegische Küste aber auch Ephyren für den Herbst bekannt sind (BROWNE 1904, p. 31–32) und zwar aus der Umgebung von Bergen aus dem September: vom 2. IX. 1898 (4 mm), 24. IX. 1902 an zwei Stellen (1 Ex. 7 mm; 4 Ex., von denen 3 kleine Ephyren, das vierte 10 mm). Solange keine ausführlicheren Beobachtungen vorliegen, lässt sich nicht sagen, ob *Aurellia* sich da den ganzen Sommer hindurch fortpflanzt oder nur im Frühling und Herbst (vergleiche das unter *Cyanea capillata* gesagte) [1]).

Fassen wir diese Beobachtungen zusammen, so finden wir die Ephyren in Süd- und Westengland Januar bis April, in Holland wahrscheinlich Februar bis Juni, an der Küste Norwegens jedenfalls im März, an der Ostküste von Jütland März oder April bis Juni, in der Ostsee bei Hel und im Finnischen Meerbusen im Mai–Juni. Das bedeutet eine deutliche Verspätung nordostwärts, mit der das frühe Datum für Ephyren an der Küste Norwegens nicht im Widerspruch steht, da die Wassertemperatur hier relativ hoch ist. Bei Helgoland sollten die Ephyren im Dezember–Januar, bei Kiel von Ende Januar bis Ende April vorkommen, was einer allmählichen Verspätung nordostwärts widersprechen würde. Ich nehme an, dass, was Helgoland betrifft, eine Verwechslung mit *Cyanea* vorliegt, denn die Angaben über das Vorkommen der jungen Aurellien dort sind wohl sicher unrichtig, sieh weiter unten. Was Kiel angeht, so ist es, wie oben gesagt, ebenfalls vielleicht nicht sicher, dass die Angabe richtig ist. Ich zweifle deshalb nicht daran, dass die Verspätung für das Vorkommen der *Aurellia*-Ephyren Tatsache ist. – Im Zusammenhang damit ist von Interesse, dass die Ephyren dieser Art im Mittelmeer (Golf von Triest) im Oktober geboren werden (GRAEFFE, 1884).

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[1]) Dr. P. KORRINGA, Bergen op Zoom, verbunden am Institut für Fischereiforschung, fand am 4. XI. 1941 in der Nähe von Yerseke (Prov. Zeeland) strobilierende Scyphistomen auf jungen Austern des Brutfalls 1940. Nachdem sie etwas länger als eine Woche im Laboratorium gehalten waren, kamen Ephyren frei, die zur *Aurellia* gehörten. „Vielleicht hat die ziemlich hohe Temperatur ihre Abschnürung begünstigt". Dies bedeutet wahrscheinlich, dass *Aurellia* auch in Holland im Herbst Strobilation zeigen kann, obgleich die Strobilation normal im Frühjahr stattfindet. Da die Medusen an der holländischen Küste meines Wissens nicht nach Ende September gefunden werden, so ist es wahrscheinlich, dass diese im Herbst geborenen Ephyren ungünstigen Umständen zufolge als Regel nicht zu Medusen heranwachsen.

J. VIERGEVER, Serooskerke, Insel Schouwen, teilt mir mit, am 5. II. 1939 eine *Aurellia*-Meduse von ungefähr 8 cm Diameter an der Küste dieser Insel gefunden zu haben. Diese mag als Ephyre spät im Herbst abgeschnürt sein. Daraus könnte man folgern, dass Exemplare der Herbstgeneration dann und wann tatsächlich heranwachsen.

Nehmen wir also die Verspätung von Südengland (Januar–März) über Holland (Februar–Juni) und Dänemark (März–Juni) nach der Ostsee (Mai–Juni) als sicher an, so fällt die Zeit der Ephyrenabschnürung mit einer Wassertemperatur von ungefähr 4–11° zusammen. Auch für diese Art muss deshalb gelten, dass sie in Südengland, wo die Wassertemperatur erst in der letzten Dekade des Dezember unter 11 und kaum unter 8° sinkt, erst ziemlich spät eine für die Ephyrenbildung günstige Temperatur findet.

Nicht die Abschnürung der Ephyren, sondern der Anfang der Strobilation soll eigentlich bei der Untersuchung der Periodizität studiert werden. Dieser wiederum könnte vom Zustand der Scyphistoma in den vorangegangenen Monaten abhängen und in dieser Weise könnte eine „innere" Periodizität vorgetäuscht werden. In dieser Hinsicht sind die Bemerkungen THILLS (1937, p. 92) von Interesse, der angibt, dass in den Becken des Berliner Aquariums die Scyphistomen im März zu strobilieren anfingen, „ohne dass die Temperatur, Fütterung oder Belichtung geändert worden war; die in Frage kommenden Becken werden das ganze Jahr über bei gleicher Temperatur gehalten und nur künstlich beleuchtet". Dies besagt nichts weniger als dass die Annahme, die Temperatur sei hier von grossem Einfluss, nicht stimmt. Diesen Angaben stehen aber die Mitteilungen HAGMEIERS (1930, p. 554) gegenüber, nach denen die Temperatur von grossem Einfluss auf den Beginn der Strobilation sein mag; „unsere eigenen diesbezüglichen Versuche sind noch nicht abgeschlossen, machen es aber wahrscheinlich, dass die obere Grenze, bei der eine Strobilation der Nordseetiere stattfindet, etwa bei 9 bis 10° C liegt. Unsere im Sommer 1928 entstandenen, unter guten Bedingungen bei 13 bis 15° C gehaltenen Scyphistomakulturen zeigten den Winter über keinerlei Neigung zur Strobilation, sondern bildeten immer neue Polypen, während die bei niedrigerer (4 bis 10° C) Temperatur gehaltenen älteren Kulturen strobilierten". Es fällt auf, dass die Angabe 4–10° C für die Strobilation der *Aurellia*-Scyphistomen gut mit unserer Schätzung 4–11° C als günstige Temperatur für die Ephyrenbildung draussen stimmt. Eine Stütze für HAGMEIERS Standpunkt bildet diese Übereinstimmung natürlich nicht, VAN DER MAADENS Material enthält aber in anderer Form eine solche Stütze. Bei der Behandlung der *Cyanea lamarckii* wies ich schon darauf hin, dass für *Aurellia*, *Chrysaora* und *Rhizostoma* wahrscheinlich ist, dass die Temperatur die Periodizität beeinflusst. Vergleicht man die Figur 3 VAN DER MAADENS mit den Diagrammen der Meerwassertemperaturen für die niederländischen Feuerschiffe (Fig. 2), dann findet man 1934 eine sehr grosse Häufigkeit der *Aurellia* zwischen Ende Mai und dem 10. Juli, dann auf einmal keine mehr. Die Meerwassertemperatur des Winters 1933–'34 war sehr niedrig und man könnte sich vorstellen, dass die Strobilation glatt verlief und sich dadurch nicht über eine längere Periode erstreckte. Dadurch wäre dann die Periode der Medusen zu einem baldigen und abrupten Ende gekommen. 1935 war *Aurellia* wenig zahlreich und die Periode des Vorkommens erstreckte sich über eine sehr lange Zeit, bis Ende September. Die Temperatur im Winter '34–'35 war bis zum Mai abnormal hoch und wenn niedrige Temperatur wirklich eine glatte Strobilation zur Folge haben sollte, so dürfen wir einen entgegengesetzten Einfluss des Winters '34–'35 annehmen. 1937 ähnelt im Auftreten der Medusen und was die Temperatur im Winter '36–'37 anbelangt dem Jahre 1935 ein wenig. Die Jahre 1933 und '36 sind sich mehr oder weniger untereinander gleich im ziemlich plötzlichen Verschwinden der Medusen und auch in ihren Wintertemperaturen. Die Höchstzahl der Medusen fiel 1933 Anfang, 1936 Ende Juni. Das späte Maximum Ende Juni im Jahre 1936 mag mit dem relativen Temperaturfall im April '36 zusammengehangen haben. Wie dem auch sei, es ist wahrscheinlich, dass ein gewisser Zusammenhang zwischen der Temperatur während der Strobilations- oder Ephyrenbildungsperiode und der Zeit des Auftretens der Medusen wirklich besteht.

USSINGS Beobachtungen scheinen darauf hinzuweisen, dass die

Lösung der Ephyren von Temperaturerhöhung begünstigt wird; die Wahrnehmungen sind aber nicht beweisend und der Einfluss äusserer Einflüsse auf die Knospenbildung, Strobilation und Ephyrenabschnürung sollte für die verschiedenen Arten einmal gut untersucht werden. Nach CLEVE (in HAGMEIER, 1930, p. 558) „lässt sich die Ephyra von *Aurellia* noch gut bei 5° pflegen; sinkt die Temperatur auf 3°, so bleiben die Tiere am Leben, aber sie fressen nicht mehr; bei –2° sterben die Ephyren".

Einige Angaben über die geringen Ansprüche, welche die Scyphistomen von *Aurellia* an ihre Umgebung stellen, werden von HALISCH (1933, p. 298–300) gemacht. „Überhaupt ist die Widerstandsfähigkeit dieser Scyphopolypen ausserordentlich gross. Sie halten nicht nur im trüben Wasser gut aus, sondern auch konzentriert salzhaltiges Wasser scheint ihnen längere Zeit nicht allzusehr zu schaden. Der obengenannte Polyp, der bereits strobilierte, hatte sich im Seewasser, das zum Schluss bis zur Hälfte verdunstet war, etwa ein halbes Jahr aufgehalten. Danach in frisches Wasser gebracht, trieb er, gleich den anderen Scyphistomen, Knospen hervor. Ebenso vertragen sie beträchtliche Schwankungen der Temperatur und der Intensität des Lichtes. Und zwar wurden die Kulturen in der ersten Zeit direkt der Sonne ausgesetzt, und die Temperaturen stiegen oft auf mehr als 20°. Eine Schädigung der Kulturen trat nicht ein."

Gehen wir jetzt zur Behandlung der Periodizität im Erscheinen der Medusen über, so fanden wir oben, dass die jungen Medusen bei Den Helder ab halb April, bei Katwijk von Anfang Mai an erscheinen, dass das Maximum im Mai–Juni liegt und die letzten Tiere im August oder spätestens September verschwinden.

Was Süd- und Westengland anbelangt, so kamen in Liverpool Bay 1894 sehr kleine Quallen (die grösste 18 mm) Ende April zur Beobachtung (BROWNE, 1895, p. 412). BROWNE (1906) gibt für the Firth of Clyde an, dass Aurellien von 3–10 cm da 1902 von Anfang bis Mitte Juni ziemlich zahlreich waren. Tausende waren am 20. Juni in einem der "Lochs" anwesend. Nach GARSTANG (Plymouth Marine Fauna) erscheinen die jungen Medusen bei Plymouth gegen Ende Mai, nachdem die Ephyren gegen Ende März aus dem Plankton verschwanden. Die Medusen sollten also zwei Monate nicht zur Beobachtung kommen. Sie erreichen ihre grösste Häufigkeit im Juni. Eine Zeit des Verschwindens wird nicht genannt. Bei Valencia-Harbour (Irland) scheint die Hauptzeit Mai bis Juli zu liegen (vgl. M. J. und M.

& C. DELAP 1905 und 1907), BROWNE (1900, p. 734) nennt die Medusen für 1898 für die Periode Mai bis August.

Bei Helgoland kommt *Aurellia aurita* nach HARTLAUB (1896) ab Ende Mai und bis höchstens Mitte Juli vor, meist vereinzelt, zuweilen in grösserer Anzahl. Auch HAGMEIER (1930), der als Zeit für die laichreifen Quallen den „Juli?" angibt, nennt sie für Helgoland selten. Nach THILL (p. 92) sollten die jungen Medusen da vom Januar bis Mai vorkommen, die reifen Medusen im Juni. Offenbar liegt hier ein Irrtum vor; *Aurellia* erscheint als Meduse wohl nirgends in der Nordsee vor dem April. – Im Skagerrak (AURIVILLIUS, 1898 a und b) erscheint *Aurellia* als junges Tier Anfang Mai, sie wird da wahrgenommen bis in den Januar. – USSINGS Angaben für Mariager Fjord (Ostjütland, Salinität ± 15$^0/_{00}$) besagen, dass die jungen Aurellien von 10–15 mm von Anfang Mai an zu finden sind. Ihre Grössenzunahme wurde oben schon erwähnt. Im August sind noch nur wenige reif, im September fangen die Planulae sich in den Armen zu entwickeln an. Im Oktober gibt es zahlreiche Medusen von 4–9 cm mit vollentwickelten Planulae in den Armen, im November zahlreiche tote und sterbende Aurellien, bis 12 cm gross. Sogar im Januar (den 1. Januar 1923) wurden einige mittelgrosse lebende *Aurellia*s beobachtet, teilweise defekt. Am 18. März (1923) schliesslich wurde ein mittelgrosses Tier gefunden, das nach USSING überwintert hatte. – KRAMP (1915, p. 20) nennt einige wenige sehr junge Tiere, nahe am Boden in der Nähe von Spodsberg (Kattegat) im April gefunden. – LOHMANN sagt, dass die ersten kleinen Aurellien von 1–2 cm Durchmesser bei Kiel von Anfang Mai an gefunden werden. Neben den grossen Tieren von bis 20 cm findet er aber sogar Ende Juli noch kleine von 1–10 cm Durchmesser. Er gibt eine Tabelle der Anzahlen Planulalarven im Jahre 1905. Die ersten erschienen im Juli, die letzten verschwanden Anfang November, das Maximum lag im August und September. Die ersten Planulae erschienen zugleich mit den geschlechtsreifen Tieren, es besteht also kein Zweifel über ihre Identität. – Aus einer Mitteilung von MÖBIUS (1880) geht hervor, dass *Aurellia* auch bei Kiel bis spät in den Winter hinein gefunden wird, denn MÖBIUS fand am 21. Dezember (1879) im Eis eingefrorene Exemplare, die wahrscheinlich in der Nacht vom 19. auf den 20. eingefroren waren. – Nach BOGUCKI erscheinen bei Hel die kleinen Medusen von ungefähr 1 cm erst im Juli, um dann bis Ende August heranzuwachsen und zu reifen.

Planulae gibt es da nach ihm in den Monaten September–November. – Schliesslich gibt WIKSTRÖM (1932) für die Schären von SW-Finnland das Erscheinen der kleinen Medusen für Anfang Juli an. Erwachsene Tiere kommen erst im August vor, aber sogar dann gibt es noch (offenbar viele) Tiere van 1.5–3 cm. Es wird nicht angegeben, wann die letzten Tiere verschwinden. – Es sei noch hinzugefügt, dass auch an der schottischen Küste *Aurellia* einmal im Winter (Januar) gefunden wurde (KRUMBACH 1925, p. 653). Weiter geht aus dem Vorkommen von Ephyren an der norwegischen Küste im September hervor (sieh oben), dass auch da die Medusen sich wahrscheinlich noch bis spät im Jahr vorfinden mögen.

Diese Angaben wiederum zusammenfassend finden wir eine deutliche Verspätung im Auftreten der Medusen von *Aurellia* von Süd nach Nord. Die Tiere erscheinen im Norden später, werden da später geschlechtsreif und verschwinden später. Genau wie bei *Cyanea capillata* werden an den nördlichen Fundorten einige Tiere bis spät in den Winter hinein wahrgenommen, einzelne Stücke scheinen sogar den Winter hindurch am Leben bleiben zu können. Während nun bei einer Anzahl Fische dieses spätere Vorkommen im nördlichen Teil der Nordsee dem südlichen gegenüber von den höheren Temperaturen des tieferen Wassers spät im Jahr ermöglicht wird, begegnen wir in *Aurellia* einer Art, die an Brackwasser in Küstennähe, besonders an Flussmündungen u.s.w., gebunden ist, wo im Winter so extrem niedrige Temperaturen vorkommen, dass die Tiere teilweise einfrieren. Das späte Vorkommen im Norden ist also sicher kein Vorteil für die Medusen, wie bei den obengenannten Fischen, sondern nur notwendige Folge davon, dass die Medusengeneration so spät endet. Während also das späte Vorkommen im Norden sowohl von Fischen wie von Medusen von der Verschiebung der Jahreszeiten verursacht wird, steht es für die Fische so, dass die hohen Temperaturen des tieferen Wassers, die gerade im Spätherbst erreicht werden, günstig zum Aufenthalt bis tief in den Winter hinein sind, für *Aurellia* aber so, dass sie ihrer späten Entwicklung wegen gezwungen wird bei zu niedrigen Temperaturen zu leben. In diesem Zusammenhang ist von Interesse, dass die Meduse von *Aurellia* im Mittelmeer (Golf von Triest) in den Monaten Februar bis Mai (sehr selten Juni) vorkommt; reife Eier und ausschlüpfende Planulae sind da März bis Juni zu finden (GRAEFFE 1884).

Obiges gilt genau so für Nordamerika, wovon BIGELOW (1928, p. 364) folgendes schreibt.

"In the northern part of its range one generation of Aurelia is produced each year, the winter being passed in the Scyphostoma stage, and the young medusae appearing later and later in the season from south to north, corresponding to the difference in temperature of the water with the latitude. Thus Bumpus (1898 and 1898a), Hargitt (1905 and 1905a), and Fish (1925) have found both the ephyrae and the slightly older medusae near Woods Hole from March to May. Many have grown to a diameter of 1 to 2 inches there by April (Mead, 1898) and to 4 to 5 inches by mid May, but few if any appear in Massachusetts Bay before May (we found none there during that month in 1915 or in 1920), and it is not until July that they attain their full size of 6 to 10 inches north of Cape Cod."

"According to Louis Agassiz (1862, p. 76), the Aurelia off Massachusetts become sexually mature late in July and through August, which I can corroborate, having found the mouth arms of all large adults examined at that season laden with developing eggs and planulae. No doubt they continue producing young from that time onward, through September and October, until they are destroyed by the autumn gales, which seems to be their normal fate. According to Mayer (1910), Aurelia does not mature until September in the Eastport region, but I have never seen nor heard of one in the Gulf of Maine after October.

"It is probable that the breeding season of Aurelia and the seasonal succession of its generations are not so definite in the warmer parts of its range, for I have seen large specimens in April in Santiago Bay, Cuba (according to Mayer (1910) Aurelia matures in May at Tortugas, Fla), others collected in Barataria Bay, La., during the last week in September, and half-grown individuals taken in the Indian River, Fla., as late as the second week of December."

Wir stellten oben fest, dass bei *Cyanea* eine lange Zeit zwischen der Abschnürung der Ephyren und ihrem ersten zahlreichen Erscheinen vergeht. Gleiches, obgleich in geringerem Masse, gilt für *Aurellia*. In Plymouth verschwinden nach GARSTANG (Plymouth Marine Fauna) die Ephyren gegen Ende März, während die jungen Medusen erst Ende Mai erscheinen. Sogar wenn dieses Datum zu spät angesetzt sein sollte, so bliebe dennoch ein gewisser Zeitunterschied zwischen beiden Erscheinungen [1]. An der holländischen Küste erscheinen die *Aurellias* in grösserer Zahl ab Anfang Mai und es kommen dann auf einmal, genau wie bei *Cyanea*, grosse und kleine Tiere durcheinander vor (am 29. IV. 1936 und 8. V. 1934: 5 bis 20 oder 25 cm Diameter). Die grossen Tiere sind (vergleiche oben) drei Monate alt und sie müssen also Anfang Februar als Ephyren entstanden sein. Es besteht deshalb, genau wie bei *Cyanea*, ein Intermezzo von bis ungefähr zwei Monaten zwischen der Entstehung der ersten Medusen aus Ephyren und der Erscheinung dieser Medusen im Plankton [1]. – Für Mariagerfjord sollte eine solche Zwischenzeit kaum bestehen, denn die Ephyren erscheinen Ussings Angaben zufolge so spät, dass die Medusen ihnen sozusagen gleich folgen. Wenn die Ephyren da aber statt im April im März erscheinen, was wahrscheinlicher ist, so beträgt die Zwischenzeit zwischen der Bildung von Quallen aus Ephyren und dem Erscheinen der Quallen ungefähr einen Monat. Falls Lohmanns Angaben für Kiel richtig sind, beträgt die betreffende Zwischenzeit da zwei Monate. Bei Hel sollte sie, nach den Angaben Boguckis, wiederum einen Monat betragen. Schliesslich sind Wikströms Beobachtungen (1936) von grossem Interesse. „Gewöhnlich erscheinen Quallen in den oberflächlichen Wasserschichten von Hanga erst Ende Juli und sind dabei etwa halberwachsen (40–50 mm); so verhält es sich überhaupt in den inneren Schären, wohin Tiere aus den äusseren Schären gegen Ende des Sommers kommen. Eine zufällige Beobachtung grosser Mengen von kleinen Quallen (7,5–33 mm) zwischen dem 5–7. Juli 1933 gab Anlass zu der Vermutung, dass solche in den tieferen Wasserschichten schon im Vorsommer vorkamen. Das wurde im Sommer 1934 bestätigt, wo ich mit einem in verschiedene Tiefen versenkbaren Planktonnetz nahe am Boden an allen untersuchten Stellen zahlreiche Quallen in den jüngsten Entwicklungsstadien erhielt, obgleich in den oberflächlichen Schichten keine Quallen zu sehen waren. Zwischen 27.6 und 2.7 wurden in einer Tiefe von 8–20 m in fünf Netzfängen 21, 17, 13, 20 resp. 182 Individuen gefunden, die meist 1.5–5 mm gross und somit nahe an dem Ephyra-Stadium waren. Nach dem 2.7 konnten dann nur noch einzelne Individuen gefangen werden. Ende Juli erschienen wie früher die halberwachsenen Quallen von 40 mm und darüber." Wikström untersuchte dann weiter, ob an denselben Stellen bei Hanga (die Aussenschärenkarakter haben) auch Scyphopolypen vorkamen; er fand diese wirklich. Er nimmt dann an, dass der in Bodennähe höhere Salzgehalt die jungen Tiere unten hält. Dies mag für dort zutreffen, da ein solcher Salzgehaltsunterschied aber an anderen Stellen (zum Beispiel an der holländischen Küste) sicher keine Rolle spielt, scheint es wahrscheinlicher, dass die jungen Medusen auch einer anderen Ursache wegen so lange unten bleiben können.

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[1] Dem widerspricht, dass bei Port Erin 1894 sehr kleine Quallen (bis 18 mm gross) Ende April zur Beobachtung kamen (BROWNE, 1895, p. 412).

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[1] Wir dürfen für das Heranwachsen der Ephyren, bis sie in Medusen von 10 mm Diameter metamorphosieren, ungefähr einen Monat rechnen.

Genau wie für *Cyanea lamarckii* habe ich nun auch für *Aurellia* versucht ausfindig zu machen, welcher dieser Faktor sein könnte. Dabei lag es, nach dem was für *Cyanea* gefunden war, auf der Hand, einen Zusammenhang mit Temperatursteigungen zu erwarten. Es stellte sich aber heraus, dass das Bestehen eines solchen Zusammenhangs nicht zu beweisen war, im Gegenteil, er schien ganz zu fehlen; kein einziges Mal fällt eine *Aurellia*-Zunahme mit einer plötzlichen Temperatursteigung (Fig. 2) zusammen. VAN DER MAADEN kommt zum Schluss, dass hohe *Aurellia*-Maxima, statt wie bei *Cyanea* bei westlichen Winden, besonders bei nördlichen Winden vorkommen. Und er fügt hinzu: „Im Gegensatz zu dem, was wir für *Cyanea* finden, braucht nicht erst eine Periode schönen Wetters mit östlichem Wind der Häufigkeit voran zu gehen". Unser Fund, dass *Aurellia* nicht nach Temperatursteigung zahlreich wird, stimmt also mit VAN DER MAADENS Angaben, nach denen *Aurellia* nicht nach schönem Wetter mit Ostwind zahlreich auftritt. Ich habe mich nun gefragt was wohl der Zusammenhang zwischen Wind und Anschwemmen sein dürfte. Denn VAN DER MAADENS Beobachtungen lassen keinen Zweifel darüber bestehen, dass *Aurellia* viel mehr bei nördlichen als westlichen Winden angeschwemmt wird, obgleich beide das Oberflächenwasser nach der Küste treiben. Der Zusammenhang zwischen Anschwimmen und Wind bei *Cyanea* ist vermutlich ein ganz indirekter. Die Art wird zahlreich bei einer Temperaturerhöhung und „Seewind" bringt nun die Tiere ans Land. Dreht der Wind von Ost durch Süd nach West, so könnte die grosse Mehrzahl angeschwemmt werden bevor Nord erreicht ist und so könnte der grosse Einfluss westlicher Winde entstehen. Ausserdem könnte Nordwind durch Abkühlung das Sinken der *Cyanea*s bewirken und so dem Anschwimmen entgegenarbeiten. Dreht der Wind von Südost nach Nord, so wird es meist kälter und dies könnte wiederum das Anschwimmen verhindern. Möglicherweise kommt hinzu, dass der Wind im Mai und im Juni meist mit der Uhr dreht, so dass die Westwinde dadurch mehr Einfluss als die Nordwinde ausüben können? Wenn wir nun versuchen diese Möglichkeit auf *Aurellia* anzuwenden, so wäre es also möglich, dass nördliche Winde dadurch Effekt haben, dass *Aurellia* statt auf Temperatursteigung auf Temperaturfall reagiert. Nördliche Winde gehen fast immer mit Abnahme der Lufttemperatur zusammen. Dadurch kühlt das Oberflächenwasser ab. Es sinkt und verursacht einen Temperaturfall in Bodennähe. Es ist auffallend, wie gross im Winter der Einfluss fallender Temperaturen auf Tiere (wenigstens Fische) in Bodennähe sein kann und wie schnell er wirkt. Für die Möglichkeit, dass Temperaturfall *Aurellia* herauf bringt, spricht noch eine andere Tatsache. VAN DER MAADENS Wahrnehmungen enthalten einige sehr auffallende Beispiele von massalem Anschwimmen bei Ostwind. Solche Beispiele, die eigentlich für *Cyanea* ganz fehlen, besagen, dass *Aurellia* auch in grosser Zahl von dem Bodenstrom angeschwemmt werden kann und VAN DER MAADEN besitzt denn auch einige Beobachtungen, die darauf hinweisen, dass das Oberflächenwasser bei solcher Gelegenheit wenig Aurellien enthält. Wenn nun Temperaturfall *Aurellia* an die Oberfläche bringen sollte, so könnte Temperatursteigung (die meistens bei Ostwind auftritt) gerade den umgekehrten Effekt haben und die Tiere unten halten, so dass der bei Landwind bestehende Bodenstrom sie nach der Küste führen könnte. – Es sei sofort hinzugefügt, dass später in der Saison auch *Chrysaora* und besonders *Rhizostoma* mit SO Wind angeschwemmt werden (*Rhizostoma* sogar viel). Meiner Meinung nach ist der Grund dafür aber an erster Stelle dieser, dass diese Tiere bei uns, wenn sie bis in den Herbst hinein vorkommen, gezwungen sind in zu kaltem Wasser zu verbleiben und deshalb sterben und sinken.

Die Schwierigkeit in der Annahme, dass *Aurellia* auf Temperaturfall reagiert, liegt aber darin, dass die Art erst ziemlich spät im Frühjahr „erscheint". Wie *Cyanea* vermutlich nur auf Temperatursteigung über einer gewissen Minimumtemperatur reagiert, so müssen wir also auch für *Aurellia* annehmen, dass eine gewisse Höhe der Temperatur nötig ist um die Tiere an die Oberfläche zu bringen. Es würde also Temperaturfall erst dann von Einfluss sein, nachdem eine gewisse Temperaturhöhe erreicht worden ist. An sich ist das gar nicht unmöglich, die Annahme liegt indessen auch nicht auf der Hand.

Ich habe mich vergebens bemüht einen Zusammenhang zwischen dem Anschwimmen bei nördlichen resp. östlichen Winden und der Salinität des Wassers zu finden. *Aurellia* ist, wie gesagt, eine ausgesprochene Küstenform, die im Brackwasser zu Hause ist. An der holländischen Küste, wo der Einfluss der ins Meer ausströmenden Flüsse sehr gross ist, erhöhen S bis W Winde die Oberflächensalinität, weil sie Wasser hoher Salinität nach der Küste treiben, wo es sich mit dem Flusswasser vermischt. Als Reaktion darauf könnten die Aurellien unten bleiben. N bis O Winde würden den umgekehrten Effekt haben. Ich kann aber kaum annehmen, dass dieser Umstand eine Rolle spielt, erstens weil die Salinitätsunterschiede gering sind, zweitens weil wir doch nicht ohne Temperatureinfluss auf das Erscheinen der Quallen auskommen.

Oben kamen die Unterschiede zwischen verschiedenen Jahren schon zur Sprache, wenn sie dazu benutzt wurden einen Einfluss der Temperatur auf die Strobilation wahrscheinlich zu machen. Diese Unterschiede seien jetzt noch an und für sich besprochen. Sie beziehen sich auf die Zeit und auf die Zahlen.

Was die Zeit des Erscheinens anbelangt, so sind die Unterschiede von Jahr zu Jahr so gering, dass man sich fragt ob sie – in Anbetracht der Beobachtungsmethode – beweisend sind. 1935 und '36 aber wurden die ersten Aurellien bei Katwijk am 2. und 3. Mai angeschwemmt, 1933 am 16., '37 am 21. Zusammenhang zwischen der Erscheinungszeit und der Temperatur wäre begreiflich, da die Temperatur sowohl den Anfang der Strobilation wie wahrscheinlich das Heraufkommen der Quallen beeinflusst.

Für die Hydromedusen findet KRAMP (1927, p. 222–223) denn auch das Bestehen einiger Variation im Auftreten von Jahr zu Jahr, "in many cases exhibiting actual correlation with the temperature of the water". "Only in the case of a few species is our material sufficiently representative to permit of a more or less reliable comparison between the different years; and mostly among the smaller forms, which can be taken in great numbers in the vertical hauls from the lightships; even with these species, however, there is the serious defect that the collections from Schultz's Grund lightship were not continuous. As a general rule we may say (see Special Section) that the period of occurrence of the medusae in the plankton varies most among these species which make their first appearance in winter or early spring (*Hybocodon*, *Rathkea*, *Sarsia tubulosa*), whereas those which appear about midsummer keep very nearly to the same time every year (*Purena gemmifera*, *Euphysa aurata*, *Lizzia blondina*)." Es sei beiläufig bemerkt dass gleiches für die Ankunftszeiten unserer Zugvögel (besonders der Singvögel) im Frühling gilt.

Versuche ich nun aber das frühere oder spätere Erscheinen von *Aurellia* mit der Temperatur der Erscheinungstage (Fig. 2) zu korrelieren, so finde ich eigentlich keinen Zusammenhang, denn 1933 und '35 ist der Anfang Mai etwas wärmer als normal, '34 normal, '36 zu kalt, '37 fast normal. Vielleicht spielt hier also doch das Unzureichende der Beobachtungsmethode einigermassen eine Rolle, so mag 1937 nur spät aussehen, weil die Zahl der Medusen in diesem Jahr klein ist; dies erklärt aber wahrscheinlich nicht alles. – Ich habe auch versucht das Erscheinen der Medusen mit der Temperatur in der Zeit der Strobilation zu korrelieren, dies ist aber kaum möglich, weil der Anfang der Strobilation zu wenig genau bekannt ist. In Anbetracht der Tatsache, dass die Medusen nicht gleich nach der Metamorphose erscheinen, ist aber ausserdem unwahrscheinlich, dass der Anfang der Strobilation in der Erscheinungszeit der Medusen zum Ausdruck kommt.

Was die Zeit des Verschwindens anbelangt, so liegt als Grund für sie ein Einfluss der Temperatur auf die Strobilationsperiode, wie sie oben schon zur Sprache kam, auf der Hand, weil die Zwischenzeit, in der die Medusen im Frühling am Boden liegen sollten, auf das Verschwinden der Medusen im Herbst nicht störend wirken kann. Es wurde schon darauf hingewiesen, dass ein gewisser Zusammenhang besteht zwischen der grossen Häufigkeit im Juni 1934 und dem frühen Verschwinden in diesem Jahr und zwischen der geringen Häufigkeit im Mai '35 und dem gedehnten Vorkommen in diesem Jahr. Offenbar verläuft die Strobilation eben glatt oder nicht glatt. Für *Cyanea lamarckii* wies ich darauf hin, dass es in der letzten Dekade des Juli 1936 einen Tag mit 14.000 Stück pro km gab, dann im weiteren Verlauf des Sommers fast keine mehr. Das lässt sich jetzt in derselben Weise erklären: die Strobilation verlief glatt und ergab dadurch sehr viele Medusen, aber nur für sehr kurze Zeit. Man bekommt den Eindruck, dass günstige Verhältnisse auf einmal alle Scyphistomen zur Strobilation und Ephyrenbildung bringen können, wodurch spätere Ephyrenbildung ausbleibt und die Quallen früh verschwinden. Anderseits sollten ungünstige Umstände einer massalen Bildung von Ephyren entgegen arbeiten, spätere Ephyrenbildung bliebe dadurch nicht aus und die Periode des Vorkommens wäre eine gedehnte. Eine Stütze für diesen Gesichtspunkt ist, dass ich zu ihm kam unabhängig von Kramp (1927, p. 223), der für die Hydromedusen zu einer gleichen Annahme kommt. "As regards disappearance of the stock, all species vary considerably. In the case of the gemmiferous forms it would seem as if the stock disappeared earlier when the temperature is higher, gemmation then proceeding more briskly; and there must presumably be some limit to the number of generations which can be produced". Weiter findet man eine ähnliche Erklärung für die lange Fortpflanzungsperiode verschiedener Fische im Jahre 1924 dem Jahre 1925 gegenüber bei Russell (1926 a, p. 111).

Wie bei *Cyanea lamarckii* bestehen auch Unterschiede in der Häufigkeit der Medusen in verschiedenen Jahren. Die Figuren 2 u. 3 VAN DER MAADENS zeigen, dass, während *Cyanea lamarckii* 1935 zahlreich, *Aurellia* in diesem Jahr gerade sehr wenig zahlreich war. *Aurellia* war sehr zahlreich im Jahre 1934, *Cyanea* war dieses Jahr dagegen wenig zahlreich. Auch die anderen Jahre sind mit diesem entgegengesetzten Verhalten nicht im Widerspruch, nur 1937 hatte wenig *Cyanea* wie *Aurellia*. Bei *Cyanea* wies ich auf einen eventuellen Zusammenhang zwischen ihrer Häufigkeit im Jahre 1935 und den hohen Temperaturen im Winter 1934–'35 hin. Dieser Zusammenhang kann also für *Aurellia* nicht bestehen, man könnte im Gegenteil annehmen, dass die ziemlich niedrigen Temperaturen des Winters 1933–'34 mit ihrer Häufigkeit im Jahre 1934 und die hohe Temperatur des Winters '34–'35 mit ihrer geringen Häufigkeit im Jahre '35 zu schaffen haben. Obgleich zwei solcher Fälle wenig beweisen, wäre dieser grosse Unterschied *Cyanea* gegenüber nicht unmöglich, da schon der Zusammenhang Temperatur-Strobilation auf die Günstigkeit niedriger Temperaturen für *Aurellia* hinwies. Unsere Annahme betreffs *Cyanea*, dass eine bestimmte Temperatur in erster Linie die Knospenbildung günstig beeinflussen könnte und dadurch die Zahl der Medusen, kann für *Aurellia*, was die niedrigen Temperaturen anbelangt, nicht zutreffen. Zwar scheint bei ihr die Knospenbildung sehr ausgiebig zu sein (vgl. M. J. DELAP. 1907, p. 22–23, HAGMEIER, 1930, p. 553, HALISCH, 1933), nach HAGMEIERS Beobachtungen findet sie aber besonders im Herbst, über 10° C, statt. Wir müssen also wohl annehmen, dass es allererst der Einfluss der niedrigen Temperatur auf die Strobilation ist, die die hohen Zahlen der Medusen verursacht. Die Möglichkeit, dass daneben die niedrige Temperatur günstig auf die Nahrungsmenge oder ungünstig auf die Feinde von *Aurellia* wirken würde, wäre natürlich nicht auszuschliessen.

4. *Chrysaora hysoscella* (L.)

Die *Chrysaora*-Beobachtungen für Den Helder wiesen aus, dass diese Qualle Mitte (wahrscheinlich 1. Hälfte) Juni erscheint. Grössere Anzahlen kommen schon in der 2. Junihälfte vor, aber diese beziehen sich alle auf Tiefenfänge. Obgleich damit nicht gesagt sein soll, dass die Tiere an der Oberfläche wirklich fehlten, könnte ein relativ häufigeres Vorkommen in tieferen Schichten der Grund sein, weshalb die Art bei Katwijk im Juni selten ist. VAN DER MAADEN hat nämlich nur 2 Juni-Stücke: eins von 2 cm vom 1. Juni 1935, noch im *Pelagia*-Stadium, und ein zweites (von 15 cm Durchmesser) vom 20. Juni 1936. Während *Chrysaora* aber offenbar bei Den Helder im Juli ziemlich viel vorkommt, auch an der Oberfläche, hat V. D. MAADEN nur Juli-Tiere im Jahre 1937, sonst hat er keine vor dem 8. August. Dies mag darauf hinweisen, dass die Art bei Katwijk überhaupt später zu erscheinen anfängt. Der eventuelle Grund hierfür kommt unten zur Sprache. – Nach den Wahrnehmungen bei Katwijk liegt die Hauptzeit des Auftretens von *Chrysaora* im August-Oktober, aber 1935 kamen keine Tiere nach Ende September zur Beobachtung. Dagegen wurden 1933, '34 und '37 noch einige bis ziemlich viele Tiere im November und '33 und '34 sogar mehrere im Dezember (bis zum 7. des Monats) beobachtet, vergleiche VAN DER MAADENS Fig. 4. In Den Helder kamen Oktober-Funde nur 1932 vor, der späteste Fund ist der 24. November 1933; obgleich negative Daten nicht allzuviel beweisen, ist es nicht ausgeschlossen, dass die Art bei Den Helder nicht nur früher anfängt, sondern auch früher verschwindet als bei Katwijk.

Diese Zusammenfassung zeigt, dass *Chrysaora* bei Katwijk früh anfing im Jahre 1937, spät verschwand besonders 1933 und '34, während sie bei Den Helder wahrscheinlich spät verschwand in den Jahren '32, '33 und '34; die betreffenden Beobachtungen sind indessen wohl sehr unvollständig.

Wie gesagt gibt es in der Regel in Katwijk keine Chrysaoren vor dem August. Kleine und grosse kommen dann zusammen zur Beobachtung. Nach dem was wir für die anderen Arten fanden, scheint es selbstverständlich, dass die Tiere sich bis so lange unten, am Boden, aufhielten. Die Juli-Tiere, die nur in einem Jahr in Katwijk zur Beobachtung kamen, waren gross (sogar auffallend gross) und auch für diese wäre anzunehmen, dass sie sich bis zu der Zeit unten aufhielten. Gleiches gilt für eins der zwei Juni-Stücke. – Das Alles stimmt aber gar nicht, wenn wir auf Den Helder achten. Da erscheinen die Chrysaoren viel früher, schon Mitte Juni oder jedenfalls Anfang Juli, auch an der Oberfläche. Und da der Temperatur-Unterschied zwischen Katwijk und dort sehr gering sein muss, fragt man sich weshalb die Quallen, wenn sie wirklich anwesend sein sollten, nicht auch in Katwijk früher die Oberfläche aufsuchen. Eine andere Möglichkeit wäre denn auch, dass sie wirklich bis zum August bei Katwijk fehlen, auch am Boden. Dies wäre dann so zu erklären, dass sie bei Katwijk, im Gegensatz zu Den Helder, nicht entstehen und erst von anderswo her Katwijk erreichen. Da die Eigenbewegung der Quallen gering ist, käme dabei nur ein passiver Transport in Frage. Und da die allgemeine Wasserbewegung an der holländischen Küste entlang nordwärts gerichtet ist, könnten sie praktisch nur aus dem Süden kommen. Der auffallende Unterschied zwischen Katwijk und Den Helder wäre also so zu erklären, dass, während Katwijk seine Medusen aus dem Süden bekommt, die Umgebung von Den Helder sie selbst liefert. Ein solcher Unterschied wäre gar nicht unmöglich in Anbetracht der Tatsache, dass die Umgebung von Den Helder durch ihren Reichtum an Stein und Holz (Deiche, Hafenwerke, u.s.w.) einen grossen Reichtum an Coelenteraten, wie Actinien, Hydrozoen und festsitzenden Tieren überhaupt, aufweist, während der flache Sandboden zu Katwijk festsitzenden Tieren keine brauchbare Unterlage bietet. Weiter sind bei Den Helder viel grössere Tiefen anwesend als bei Katwijk und – wenn das für die Polypengeneration von Wert sein sollte – auch die Variabilität in der Bodenstruktur (abgesehen von der Anwesenheit von Hafenwerken, u.s.w.: Reichtum an Schlamm, Diluvialsteine, Muschelbänke) ist bei Den Helder eine viel grössere. – Natürlich könnten diese Vorteile von Den Helder Katwijk gegenüber ebensogut für die Polypengeneration von *Cyanea* und *Aurellia* gelten, offenbar ist das aber nicht der Fall, denn nichts im Auftreten dieser beiden Arten weist auf Unterschiede zwischen beiden Lokalitäten hin, ausser dem eventuell früheren Erscheinen von *Aurellia* bei Den Helder, wo die Art im grossen Brackwassergebiet der Umgebung zahlreicher sein mag als bei Katwijk.

Auch für *Chrysaora* kennen wir die Wachstumsgeschwindigkeit durch Beobachtungen von Fräulein DELAP (1901). Sie fand folgende Grössenzunahme für ein Tier, dessen Aufzucht ausserordentlich schön gelang.

Datum	Anzahl Tage	Grösse in cm
3.–4. April		Ephyren (2 mm) gelöst
22. April	18	1.3
16. Mai	42	3.8
22. Mai	48	6.3
4. Juni	61	9.4 (Farbe erscheint)
21. Juni	78	16.2
8. Juli	95	22.5

Das bedeutet, dass eine Grösse von ± 10 mm in vielleicht gut 2 Wochen erreicht wurde und dass das Tier einen Durchschnitt von 22.5 cm erreichte in ungefähr 3 Monaten. Letzteres fanden wir auch für *Aurellia*. Eine Grösse von ± 10 mm wurde aber bei *Cyanea* und *Aurellia* in ungefähr 4 Wochen erreicht, *Chrysaora* wuchs also in der ersten Zeit sehr viel schneller als diese, was teilweise der höheren Temperatur (im Mai und Juni 15–17° C) zuzuschreiben gewesen sein mag.

Das grösste Juni-Tier von VAN DER MAADEN (vom 20. IV. 1936) mass ungefähr 15 cm. Das besagt, dass dieses Tier zwei bis drei Monate alt war und es mag also zwischen Mitte März und Mitte April als Ephyre entstanden sein. VAN DER MAADEN beschreibt ausführlich die Grösse der Tiere, die er 1937 im Juli fand (15.–21. VII.). Diese waren auffallend gross: „Die Schirmbreite der meisten Exemplare war über 20 und mehrere Exemplare erreichten sogar eine Breite von ungefähr 30 cm". Es ist anzunehmen, dass diese Tiere mindestens drei Monate alt, also spätestens um Mitte April als Ephyren abgeschnürt waren. Das Tier VAN DER MAADENS im Pelagiastadium, vom 1. Juni 1937, das einzige kleine Tier, das VAN DER MAADEN vor dem August fand, mag einen Monat alt gewesen und Anfang Mai geboren sein. – Daneben wurden in Katwijk zahlreiche junge Tiere bis in den Oktober, einige sogar bis in den November hinein gefunden und es ist gewissermassen auffallend wie viel kleine Tiere gerade im Herbst (September–Oktober) gefunden wurden. Da diese Tiere nicht viel grösser als 2–3 cm waren, müssen viele Ephyren erst im Spätsommer, Juli bis September, abgeschnürt worden sein. Das ergäbe für die Medusen von Katwijk also eine Geburtsperiode von April bis September.

Bei Den Helder kommt *Chrysaora* ziemlich viel in der zweiten Junihälfte und im Juli vor und ich glaube nicht nur in der Tiefe, sondern auch an der Oberfläche. Wenigstens war die Art Anfang Juli 1932 in grosser Zahl im Oberflächenwasser des Nieuwediep zu finden. Ich habe seinerzeit leider keine Masse notiert, aber soviel ich mich entsinnen kann, war ein grosser Teil dieser Tiere klein, vielleicht nicht älter als einen bis zwei Monate. Diese wären also im Mai bis Anfang Juni geboren. Bis wie gross die grösseren unter diesen frühen Tieren waren, kann ich mich nicht entsinnen. Sie müssen aber mindestens zwei Monate alt gewesen und also Anfang April geboren sein. Genau wie bei Katwijk sind unter den späten Tieren von Den Helder kleine wahrscheinlich relativ stark in der Mehrzahl, wenigstens waren die meisten Oktobertiere von 1932 klein und sogar am 24. November '33 wurde, ausser einem Tiere von 15 cm, noch eins von 5 cm gefunden. So ein Tier ist wahrscheinlich im September entstanden. Auch die Wahrnehmungen für Den Helder weisen also auf eine Geburtsperiode von (Anfang) April (vielleicht früher) bis September hin. Daraus geht hervor, dass die Ephyren später als bei *Cyanea* und *Aurellia* abgeschnürt werden, denn die von *Cyanea lamarckii* entstehen vom Januar bis in die zweite Hälfte von Juni, die von *Aurellia* Februar bis Juni.

In Valencia Harbour kommen die Medusen der *Chrysaora*, nach den Beobachtungen BROWNES (1900) und M. & C. DELAPS (1905 und 1907) vom Mai an vor; sie sind offenbar am allgemeinsten (obgleich unregelmässig in ihrem Auftreten) im Juni und Juli, werden einige Male für den August erwähnt, nicht für den September, und nur einmal für den Oktober (10. X. 1905). Alle im Mai beobachteten Tiere sind jung, von 2 cm ab aufwärts, solche Tiere waren besonders zahlreich Ende Mai und Anfang Juni 1902, das früheste Datum war der 7. Mai (M. & C. DELAP, 1907, p. 4 und 13). Grosse Stücke erscheinen von Mitte Juni an. Diese Beobachtungen zeigen, dass die Ephyren von Anfang April an frei kommen, wie auch Scyphistomen im Aquarium Anfang April Ephyren abgaben. – Für the Isle of Man (MOORE, 1937) scheint *Chrysaora* nicht festgestellt zu sein, aber nach BYERLEY kommt sie bei Liverpool, und zwar in den Monaten Juli und August, selten vor, und WALTER nennt sie da "frequently very common" (BROWNE, 1895, p. 412). Nach KRAMP (1937) ist das der nördlichste Fundort an der Westseite von Grossbritannien. – In the Plymouth Marine Fauna wird für Plymouth nur angegeben: "Occasionally during the summer months. Planulae liberated in Aug. and reared to Scyphistoma stage".

Für Helgoland gibt HARTLAUB die Art für Ende August bis Anfang Oktober an, HAGMEIER nennt als Zeit für das Vorkommen der laichreifen Quallen August bis September. HARTLAUB scheint anzunehmen, dass sie nicht jeden Sommer bei Helgoland vorkommen. In Zuchtversuchen wurde Strobilation im März, Lösung der Ephyren Anfang April beobachtet. Aus den Angaben KÜNNES (in KRAMP, 1934, p. 214) geht hervor, dass im Juli 1925 Quallen aller Grössen, von 8 mm Diameter an, bei Helgoland gefunden wurden. Leider wird die Grösse der grössten Tiere nicht angegeben, sie müssen aber mindestens zwei Monate alt gewesen und also spätestens im Mai geboren sein, vielleicht früher.

Nach KRAMP (1934 und 1937) ist *Chrysaora* selten an der Westküste von Jütland und bis Skagen. Sogar 1925, als sie bei Helgoland ziemlich zahlreich war, wurde sie nicht nördlich von Horns Rev (± 55° 35′ N) beobachtet (wohl, und zwar im Oktober, an 5 Stationen S und SW von Horns Rev); den 7. Oktober 1926 wurde ein Exemplar am Eingang des Limfjords gefunden; Ende September und Anfang Oktober 1930 wurden zahlreiche Chrysaoren von 3 bis 24 cm Grösse östlich von 6° O.L. zwischen 55°30′ und 57°30′ N gesehen. "Many were caught in the ring-trawl with 50–100 m of wire out, and several were also seen swimming at the surface in the smooth water in the bright sunshine". Endlich wurde die Art im Jahre 1933 in der ersten Septemberhälfte in ziemlicher bis grosser Anzahl an der jütischen Westküste, nördlich bis Hirtshals, gesehen; Ende September war sie bei Hirtshals noch allgemein, die letzten wurden am 14. und 15. Oktober bei Frederikshavn (S von Skagen) gesehen. Ein Tier von nördlich von Skagen wird noch für den 28. Oktober 1923 erwähnt. (Für alle diese Angaben sieh KRAMP, 1934). – 1896 wurden zahlreiche *Chrysaora* im Oktober wahrgenommen an der schwedischen Skagerrakküste (AURIVILLIUS, 1898 b). – Aus den von KRAMP für die Tiere von Ende September 1930 genannten Massen lässt sich schliessen, dass sie im Juni bis Mitte August geboren sein mögen.

Chrysaora wird von KRAMP und DAMAS (1925; vergleiche auch KRAMP, 1934, p. 212) für die norwegische Küste aufgeführt, Datum und Fundort sind aber nicht publiziert worden.

Zusammenfassend ergibt sich folgendes. Ephyren wurden bei Valencia (Irland) von Anfang April an gefunden, in Holland müssen sie von Anfang April (oder früher) bis September entstehen, bei Helgoland 1925 wahrscheinlich vom April an, an der dänischen Westküste 1930 vom Juni bis in den August. Hieraus lässt sich, was Verspätung betrifft, wenig Sicheres schliessen. Die Medusen erscheinen bei Valencia im Mai (alle jung), bei Den Helder (wahrscheinlich teils gross) von der zweiten Junihälfte oder Anfang Juli an (bei Katwijk viel später), bei Helgoland ebenso vom Juli an (teils gross), für westlich von Jütland sind keine Daten von vor dem September bekannt. Dies weist auf eine Verspätung im Erscheinen der Quallen nordwärts hin. – Die Medusen verschwinden bei Valencia vermutlich im Oktober (nur eine Beobachtung), in Holland bei Katwijk im November oder sogar im Dezember, bei Den Helder Oktober bis November, bei Helgoland bis Anfang Oktober, an der dänischen Westküste im Oktober, an der schwedischen Skagerrakküste wurde sie 1896 im Oktober beobachtet. Hieraus lässt sich nicht allzuviel schliessen, man bekommt aber den Eindruck dass von einer sehr auffallenden Verspätung nordwärts, wie sie z.B. bei *Aurellia* eine Rolle spielt, hier nicht die Rede sein kann.

Die Scyphistomen von *Chrysaora* müssen imstande sein sehr niedrige Temperaturen zu vertragen, denn die Temperaturen des Winters 1924–'25 in der Helgoländer Bucht (1925 wurde *Chrysaora* da, wie wir sahen, viel geboren) sanken im Februar bis ungefähr 5° C, vgl. Kapitel IV.

Einige Angaben über die Ansprüche, welche die Scyphistomen der *Chrysaora* an ihre Umgebung stellen, macht CHUIN (1930) unter „matérial et élevage": „Les scyphistomes n'aiment pas la lumière. Dans mon élevage ils étaient toujours tenus à l'abri de celle-ci. La température ne doit pas dépasser ± 20° ou descendre au-dessous de 10°; au delà de ces limites de température les Scyphistomes n'accomplissent pas leur évolution habituelle; ce sont surtout le bourgeonnement et la strobilation qui sont compromis, bien que les animaux puissent résister à une variation plus grande de température". Hieraus lässt sich aber leider nicht allzuviel folgern.

Es kommt bei den Scyphistomen von *Chrysaora* Knospenbildung vor (HADZI, 1909, p. 20–22), aber welche Rolle sie spielt, ist mir unbekannt.

Für Holland findet man eine gedehnte Periode des Vorkommens kleiner Medusen, von Anfang Juni bis Ende Oktober. Sogar wenn man die Jahre gesondert betrachtet, findet man (1932) bei Den Helder kleine Medusen von Anfang Juli bis Mitte Oktober. Obgleich der Anfang der Strobilation auch hier gewiss an eine bestimmte Temperatur gebunden ist, findet also die Strobilation im Ganzen wahrscheinlich innerhalb ziemlich weiter Temperaturgrenzen statt. Das Ende steht dabei aber, wie aus dem Folgenden hervorgeht, offenbar wieder deutlich unter Temperatureinfluss. Wir fanden, dass *Chrysaora* 1933 und '34 bis in den Dezember hinein vorkam. Meine Hoffnung dieses späte Vorkommen mit hoher Wassertemperatur im Spätherbst korrelieren zu können, wurde nicht erfüllt, da der Dezember des Jahres '34 zwar besonders warm, der des Jahres '33 aber sehr kalt war. Es zeigte sich indessen, dass sowohl '33 wie '34 eine lange Periode warmen Wetters im Juli bis zum Oktober hatten, die in so ausgesprochener Form den anderen Jahren fehlte. Besonders 1933 hatte abnormal hohe Meerwassertemperaturen, in der genannten Periode 1.5–2° C höher als normal. Es liegt auf der Hand das späte Vorkommen von *Chrysaora* in diesen Jahren mit der hohen

Sommertemperatur in Zusammenhang zu bringen und anzunehmen, dass die *Chrysaora*-Medusen bis in den Dezember hinein anwesend blieben nicht weil der Dezember warm war, sondern weil die Medusen bis so spät in den Herbst hinein gebildet werden konnten. Der Fall ist vollkommen vergleichbar mit dem späten Verschwinden im Norden, dem wir bei *Cyanea capillata* und *Aurellia aurita* begegneten. Auch sie verschwanden – so war unser Schluss – nur spät, weil die Temperatur so spät im Sommer noch genügend hoch zu ihrer Bildung war. *Chrysaora* bildet nun eine unerwartete Stütze für diesen Gesichtspunkt. Es sieht wirklich aus alsob *Chrysaora* strobiliert, solange die Wassertemperatur eine gewisse Höhe hat, wie hoch möchte ich nicht entscheiden, da Anfang und Ende der Strobilation nur ungefähr bekannt sind und wir nicht genau wissen, *wo* die Medusen geboren werden. Jedenfalls aber steht der deutliche Unterschied in der für die Strobilation günstigen Temperatur für *Chrysaora* und *Aurellia* fest [1]). – Was letzten Endes die Ursache für das lange Währen der Strobilationsperiode von *Chrysaora* betrifft, so gelten für sie die gleichen Erwägungen die wir schon für *Cyanea lamarckii* erwähnten.

Wir fanden für *Cyanea lamarckii* und *capillata* und für *Aurellia aurita* bei uns und nördlicher eine lange Periode zwischen dem Entstehen und dem Erscheinen der Quallen. Jetzt finden wir eine solche Periode auch für *Chrysaora*, von der, wenigstens bei Den Helder und Helgoland, auf einmal kleine und grosse Tiere zusammen erscheinen. Dahingegen sind die ersten *Cyanea*, die RUSSELL (1931 b) im April bei Plymouth findet, alle jung, ebenso die ersten Chrysaoren, von M. & C. DELAP bei Valencia und wahrscheinlich auch die ersten *Aurellia*, von BROWNE (1895) bei Port Erin gefunden. Bei ihnen verläuft also wenig Zeit zwischen der Entstehung der jungen Medusen und ihrem Erscheinen an der Oberfläche [2]). Schon unter *Cyanea lamarckii* wurde BIGELOW zitiert, der auf einen ähnlichen Unterschied für die Medusen der *Cyanea arctica* (= *capillata*) von Woods Hole und von dem Golf von Maine hinwies. Nachdem wir diese Beispiele kennen gelernt haben, dürfen wir vielleicht annehmen, dass der Unterschied mit Temperaturunterschieden zwischen südlicher und nördlicher gelegenen Lokalitäten zusammenhängt. Es ist deutlich, dass die Strobilation bei viel niedrigeren Temperaturen anfangen kann als das Heraufkommen der Medusen. Wo diese niedrigen Temperaturen fehlen, ist der Unterschied zwischen Strobilations- und „Erscheinungs"-Temperatur gering und kann das Erscheinen der Metamorphose der Medusen bald oder gleich folgen.

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[1]) Auffallend genug gibt es in der Adria sehr wenig Unterschied in der Zeit des Auftretens zwischen *Aurellia* und *Chrysaora*, denn nach GRAEFFE (1884, p. 342) findet man die Ephyren im September–Oktober und die geschlechtsreifen Quallen vom Januar bis in den April, während Ephyren von *Aurellia* im Oktober, geschlechtsreife Tiere in den Monaten Februar bis Mai (sehr selten Juni) vorkommen.

[2]) Im Zusammenhang damit ist vielleicht von Interesse, was AGASSIZ & MAYER (1898, p. 5–6) von *Dactylometra quinquecirrha* (Desor), einer nahen Verwandten von *Chrysaora*, sagen. "When the medusae are confined in the stale water of an aquarium they often assume the position shown in Plate V, where the disk is flattened out to an extreme degree, the palps are spread

Wenn die Quallen einmal anwesend sind, so gibt es, wie bei den anderen Arten, grosse Unterschiede in der Anzahl von Tag zu Tag. VAN DER MAADEN kommt zu dem Schluss, dass *Chrysaora* in dieser Hinsicht *Cyanea* ähnelt, die besonders bei Seewind nach heissem Wetter angeschwemmt wird. Für Den Helder war die schnelle Zunahme der Anzahl bei warmem Wetter Anfang Juli 1932 sehr auffallend (sieh Beobachtungen); schon damals schien mir Zusammenhang mit der hohen Temperatur naheliegend. Ich habe also versucht die Maxima bei Katwijk mit der Temperatursteigung zu korrelieren und obgleich dies, der Dürftigkeit des Materials wegen, eigentlich schlecht gelang, habe ich doch den Eindruck, dass der Zusammenhang besteht und dass die *Chrysaora*-Medusen bei Temperaturerhöhung die Oberfläche aufsuchen.

Auffallend genug verspätet sich die Zeit des Verschwindens der *Chrysaora* eigentlich gar nicht, obgleich die Quallen nordwärts doch später erscheinen. Die Periode des Vorkommens der Quallen wird also nach dem Norden hin kürzer. Der Grund für diesen Unterschied zwischen *Cyanea* und *Aurellia* einer- und *Chrysaora* andrerseits mag wohl der sein, dass die *Chrysaora*-Medusen an so hohe Temperaturen gebunden sind, dass sie die niedrigen Temperaturen des Frühwinters gar nicht vertragen und deshalb sterben. Zum Einfrieren, wie bei *Aurellia*, kommt es gar nicht. Die gleiche Ursache, die macht dass *Chrysaora* so wenig weit nördlich vorkommt, macht auch, dass sie im Norden, wenn sie nicht in etwas wärmerem Wasser grösserer Tiefe lebt,

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out over the floor of the aquarium, and the tentacles droop listlessly downward. In this position the medusa often remains motionless for a long time, and one is almost forced to compare it with a round flat table supported upon numerous legs."

früher verschwinden muss. Man sehe aber auch was unter *Rhizostoma* über diese Sache gesagt wird.

Zuletzt sei der Unterschied in Häufigkeit zwischen verschiedenen Jahren erwähnt. Auch in dieser Hinsicht ist das Material dürftig, und zwar wegen der geringen Häufigkeit dieser Art überhaupt. Man darf vielleicht annehmen, dass sie zahlreicher war im Jahre 1936 als in den anderen Jahren. Dieses Jahr (Fig. 2) liegt mit seiner Temperatur der mittleren Temperatur für die Periode 1921–1937 am nächsten, eine eventuelle Ursache für die Häufigkeit kann ich also sicher nicht aus der Temperatur ablesen.

5. *Rhizostoma pulmo* (Macri)

Rhizostoma erscheint bei Den Helder von der zweiten Junihälfte an. Tiere im Oberflächenwasser wurden ab Anfang Juli gesehen, womit ich nicht sagen will, dass sie nicht früher vorkämen. Die frühen Tiere waren teils (vielleicht zum grössten Teil, so viel ich mich entsinnen kann aber nicht alle) klein bis sehr klein, vielleicht 1–10 cm im Durchschnitt; wahrscheinlich kommen solche aber nicht jedes Jahr, oder nicht jedes Jahr so früh, zur Beobachtung. Es ist sehr auffallend, dass diese kleinen Tiere in Katwijk, wo doch so viel ausführlichere Beobachtungen gemacht wurden, nie vorkamen. *Rhizostoma* erscheint da erst im August und gleich von Anfang an als grosses, oder jedenfalls grösseres Tier. Nach den Beobachtungen in Katwijk fällt die Hauptzeit des Auftretens September-Oktober, 1933 und '34 wurden aber, genau wie von *Chrysaora*, noch sehr spät Tiere notiert: bis zum 20. resp. 21. November. Den Helder hat keine Daten nach dem 30. X. (1932).

Da ich über die Wachstumsgeschwindigkeit der *Rhizostoma* keine Angaben habe finden können, ist es unmöglich aus der Grösse der Medusen Schlüsse auf die Zeit ihrer Entstehung zu machen. Wir können aber sicher annehmen, dass die kleinen Tiere, die bei Den Helder Anfang Juli zur Beobachtung kommen, mindestens einige Wochen alt und also spätestens im Juni entstanden sind [1]). P. J. KIPP, Utrecht, der viel an der Zoologischen Station arbeitete, teilt mir mit, dass kleine *Rhizostoma*s Ende August zahlreich vorkommen können. Das weist auf Ephyrenbildung während einer Periode von mindestens zwei Monaten hin. In den Jahren 1933 und '34 kam *Rhizostoma*, wie oben gesagt, bei Katwijk viel länger als sonst vor, bis zum 20. resp. 21. November. Da diese Novembermonate (Fig. 2) gar nicht abnormal warm waren, ist es wahrscheinlich, dass die hohen Wassertemperaturen der Periode Juli bis Oktober das späte Verschwinden bewirkten, indem sie die Bildungsperiode der Ephyren verlängerten. Mit anderen Worten, in diesem Jahr dürften Ephyren vielleicht noch bis in den Nachsommer geboren sein. Die Extremen für Ephyrenbildung wären sodann der Mai und eventuell der September.

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[1]) Nach UCHIDA (1926, p. 47–48) nehmen die Ephyren der Rhizostomen Meduse *Mastigias papua* L. Agassiz in ungefähr 20 Tagen allmählich die Form der erwachsenen Qualle an. Es wird nicht angegeben, welche Grösse sie dann erreicht haben. Aus der Beschreibung UCHIDAS geht aber scheinbar hervor, dass die Tiere in diesem Stadium gegen 8 mm gross sind. Die Wassertemperatur muss dabei ziemlich hoch sein, denn die Beobachtungen wurden in der Nähe von Misaki im Hochsommer gemacht.

Da *Rhizostoma* bei Katwijk fehlt während einer Zeit, in der sie bei Den Helder in grosser Anzahl vorkommen kann, und der Temperaturunterschied zwischen beiden Lokalitäten sicher keine Rolle spielt, müssen wir auch für diese Art wohl annehmen, dass sie Katwijk erst im Laufe des Sommers vom Süden her erreicht, während die Umgebung von Den Helder selbst ihre Rhizostomen erzeugt. Ich komme auf diesen Transport im nächsten Kapitel zurück.

Für Valencia Harbour (Irland) gibt BROWNE (1900) Tiere für Anfang September und den 10. Oktober, die DELAPS für die Periode August bis Oktober an. Sie scheinen da gar nicht regelmässig vorzukommen, was aber auch für die anderen Quallenarten gilt; 1905 waren sie indessen im ganzen September und Oktober zahlreich. Für the Isle of Man werden grosse Tiere für den April 1894 (BROWNE, 1895, p. 413) und für die Monate März, Mai und Oktober 1899 genannt (Moore, 1937: 13. Ann. Rep. Liverp. M.B.C. and Port Erin, p. 35, 1899). Daten für the Firth of Clyde sind Ende September und Ende Oktober (1901), beide Male ein Stück; nach anderen Angaben wären sie da nicht selten (vergl. BROWNE, 1906, p. 776). Für Plymouth wird nur angegeben "occasionally". Aus diesen Angaben lässt sich nicht allzuviel schliessen, aber offenbar können die (jungen?) Tiere im Süden von England ab März anwesend sein.

Von der belgischen Küste sind eine Anzahl Ephyren und junge Quallen aus den Monaten Juni und Juli (21. VI.–20. VII., sieh nächstes Kapitel) bekannt. Das stimmt mit dem, was wir für Den Helder fanden, überein.

Für Helgoland, wo die Art noch regelmässig vorkommt (vgl.

die Mitteilungen von Künne in Kramp, 1934, p. 212), wird *Rhizostoma* von Haeckel für den August und den September angegeben (Hartlaub, 1896). Stiasny (1928) hat für die Umgebung von Helgoland Ephyren und sehr kleine Quallen aus der letzten Juli-Dekade beschrieben, ausserdem eine kleine Qualle von 18 mm vom 18. August (1924). Ein ziemlich kleines Tier wurde auch im Juli 1925 gefunden (Kramp, 1934, p. 214). 1933 erschien die Art da ab Ende Juli, es wird aber nichts über die Grösse dieser Tiere gesagt (ibid., p. 217). Das Alles weist wohl auf Ephyrenbildung im Juni und Juli hin.

An der dänischen Westküste kommt *Rhizostoma* nach Kramp (1937) ziemlich regelmässig besonders im September vor. Nur selten erreichen die Tiere Skagen, Oslofjord und die dänischen und schwedischen Gewässer östlich von Skagen, 1873 wurde sie nach Möbius sogar bei Kiel gefunden (Kramp, 1934, p. 219), 1896 erreichte sie mit *Chrysaora* im Oktober in einiger Anzahl die schwedische Skagerrakküste (Aurivillius, 1898 b, p. 10) und 1933 war sie längs der jütischen Küste zahlreich und wurde sie in ziemlicher Anzahl im Skagerrak und Kattegat (auch an der schwedischen Seite: im Gullmarfjord), südlich bis Seeland, beobachtet, vgl. Kramp (1934). Die Mehrzahl kam an der jütischen Küste im September (ab den 2. des Monats) vor, die letzten wurden im Kattegat an verschiedenen Daten zwischen dem 5. und dem 25. Oktober gesehen, an der Nordküste von Seeland wurden aber noch unverletzte Stücke angeschwemmt gefunden am 21. November; in Oslofjord wurde sogar Mitte Dezember noch ein Exemplar gesehen (Kramp, 1934, p. 218–219). Auch 1929 wurde noch am 20. November ein grosses Exemplar bei Frederikshavn an der Ostküste von Jütland gefunden (Kramp, 1934, p. 215). Das früheste Datum, das ich für den Norden fand, betrifft den nördlichsten Fundort: der 12. Juli 1916, Oslofjord (Kramp, 1934, p. 213).

Zusammenfassung dieser Daten ergibt folgendes. So frühe Daten wie für the Isle of Man bekannt sind, weist die Nordsee nicht auf, ein so spätes Datum wie das für Oslofjord kennen wir nicht für südlichere Lokalitäten. Das weist auf eine Verschiebung nordwärts hin. Diese Verschiebung ist aber wohl sehr wenig ausgesprochen. Ephyrenbildung findet, nach den dürftigen Daten zu urteilen, an der belgischen Küste im Juni und im Juli statt, bei Den Helder ab Juni (oder Mai), bei Helgoland im Juni und Juli. Wenn wir annehmen, dass das Tier vom 12. Juli im Oslofjord nicht allzugross war, könnte auch dieses im Juni geboren sein. – Grössere Tiere gibt es bei Katwijk von der ersten oder zweiten Augusthälfte an (bei Den Helder kommen sie wahrscheinlich früher vor), sie sind zahlreich bis Ende Oktober (1933 und '34 kamen sie bis zum 21. November vor); bei Helgoland sind sie im August und September zu finden, an der dänischen Westküste besonders im September, östlich von Skagen 1933 hauptsächlich im Oktober, im südlichen Kattegat bis den 21. November, zugleich das späteste Datum für Katwijk. Nur im Oslofjord wurde noch Mitte Dezember ein Exemplar beobachtet. – Man bekommt den Eindruck, dass die Tiere eigentlich länger an der holländischen Küste als in der Deutschen Bucht vorkommen, aber das Beobachtungsmaterial von dort ist wohl zu unvollständig. Von der Deutschen Bucht an gibt es offenbar eine deutliche Verspätung die West- und dann die Ostküste von Jütland entlang bis an Seeland, und nordwärts nach Oslofjord. Diese Verspätung ist der Wasserbewegung zuzuschreiben; ich komme darauf im nächsten Kapitel zurück. Eine überzeugende Verspätung aller Stadien können wir, abgesehen vom früheren Auftreten der Medusen in Südengland, eigentlich nicht feststellen, und man fühlt, dass in dieser Hinsicht grosse Übereinstimmung zwischen *Chrysaora* und *Rhizostoma* bestehen muss.

Auch die Beobachtungen für *Rhizostoma* besagen, wie niedrige Temperaturen die Scyphistomen vertragen können, denn die Temperaturen für die Deutsche Bucht sind die niedrigsten der ganzen Nordsee. Es ist um so merkwürdiger, da für die Strobilation offenbar gerade sehr hohe Temperaturen notwendig sind, sieh unten.

Schon das erste Erscheinen der *Rhizostoma* so spät im Sommer, wobei kleine Medusen vermutlich die Mehrzahl ausmachen, macht es wahrscheinlich, dass eine hohe Temperatur nicht nur für die Medusen, sondern auch für die Strobilation günstig ist. Darauf weist auch das späte Verschwinden dieser Art in den Jahren 1933 und '34 hin. Die betreffenden November-Monate (Fig. 2) waren gar nicht besonders warm, wir müssen deshalb – genau wie bei *Chrysaora* – wohl annehmen, dass die hohen Wassertemperaturen der Periode Juli bis Oktober das späte Verschwinden bewirkten, indem sie die Bildungsperiode der Ephyren verlängerten. Durch diese günstigen höheren Temperaturen konzentriert sich die ganze Periode der Medusenentwicklung, stärker noch als bei *Chrysaora*, bei uns auf die wärmste Zeit des Jahres [1]. Es besteht denn auch keine lange Periode des Bodenlebens zwischen der Bildung der jungen Quallen und ihrem ersten Erscheinen. Im Gegenteil, sie kommen wahrscheinlich bald nach ihrer Entstehung an die Oberfläche. Nur ein Teil der älteren Medusen kommt deswegen bei etwas niedrigerer Temperatur im Herbst vor, weil warmes Wetter bis in den Nachsommer hinein anhalten kann und die Ephyrenbildung verlängern mag. Wie bei *Chrysaora* bestätigt dies unsere Meinung, dass die Verspätung im Auftreten der Quallen von Süd nach Nord nur notwendige Folge ihrer Wärmeliebe ist.

In Anbetracht der offenbar deutlichen Abhängigkeit der Ephyrenbildung von hoher Temperatur könnte man versucht sein anzunehmen, dass bei allen bei uns vorkommenden Temperaturen über einem bestimmten Minimum Ephyren gebildet werden könnten. Dem ist aber gewiss nicht so. Im Herbst hört die Strobilation auf, lange bevor die Temperatur erreicht worden ist, bei der die Strobilation im Frühsommer anfing, genau wie wir das bei der Fortpflanzung anderer Tierarten (Fische, Vögel) finden. Es gibt sogar für eine solche Wärme liebende Art wie *Rhizostoma* keine symmetrische Verteilung der Fortpflanzungsperiode um eine bestimmte Temperatur herum.

Die Temperatur, bei der die Medusen der *Rhizostoma* sich bei uns zum ersten Mal zeigen, ist natürlich höher als die, bei der die Strobilation anfängt. Wir fanden weiter, dass die Quallen eigentlich bis später in den Herbst hinein an der holländischen als an der dänischen Küste gefunden werden und dass eine Verspätung im Vorkommen nordwärts mindestens sehr undeutlich ist. Nur in den Gewässern östlich von Skagen finden wir wieder einige sehr späte Daten. Diese Unterschiede wären folgendermassen zu erklären. Eine für die Strobilation günstige Temperatur wird wahrscheinlich an der holländischen Küste bis später in den Sommer hinein gefunden als in der Helgoländer Bucht. Dadurch müssen die alten Tiere längs der dänischen Westküste früher als in Holland verschwinden. Die Tiere der Helgoländer Bucht werden aber bis weit in die dänischen Gewässer hinein befördert und kommen da deshalb bis später in den Herbst als an der Westseite von Jütland vor. Nicht begreiflich ist es aber, weshalb die holländischen Tiere, die doch auch vom

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[1] Dies wird noch deutlicher, wenn man bedenkt, dass die Meduse der *Rhizostoma* nach GRAEFFE (1884, p. 343) in der Adria eigentlich das ganze Jahr hindurch vorkommt, nur mit einem deutlichen Maximum in den Monaten Juni bis August.

Wasser mitgeführt werden, dann nicht bis sehr spät in den Herbst in der Helgoländer Bucht gefunden werden. Der Grund könnte sein, dass diese Tiere, unter Einfluss der niedrigen Herbsttemperaturen, bewegungslos werden, sinken und allmählich sterben, während solche Tiere im Kattegat, unter Einfluss der baltischen Süsswasserabfuhr, an die Oberfläche gebracht oder gehalten und weiter verfrachtet werden.

Es sei noch darauf hingewiesen, dass *Rhizostoma* 1933 offenbar weiter in die dänischen Gewässer vordrang als *Chrysaora*. Man könnte daraus schliessen, dass die Abhängigkeit der *Chrysaora* von niedrigen Temperaturen eine grössere als die von *Rhizostoma* ist. Das entspricht aber nicht dem früheren Erscheinen der Quallen der *Chrysaora* im Frühsommer, dem späten Verschwinden der *Chrysaora* im Herbst bei Katwijk und der südlichen Verbreitung von *Rhizostoma* überhaupt. Vermutlich bildet hier die relative Häufigkeit der *Rhizostoma* der *Chrysaora* gegenüber eine Rolle. Weiter sei auf KRAMP's Bemerkung (1934, p. 218) hingewiesen, dass *Rhizostoma* offenbar leichter als *Chrysaora* von den Wogen gegriffen und angeschwemmt wird.

Nach KÜNNE und KRAMP (KRAMP, 1934) war *Rhizostoma* bei Helgoland und an der dänischen Westküste 1933 viel zahlreicher als normal. Nach VAN DER MAADENS Beobachtungen war sie dieses Jahr aber gar nicht sehr zahlreich bei Katwijk, wo 1936 und '37 (und auch '38) viel grössere Zahlen aufwiesen. Es lässt sich annehmen, dass die Beobachtungen in Katwijk ein richtiges Bild von der wirklichen Häufigkeit im Meer geben. Ich habe erst gemeint, der Grund für diesen Widerspruch sei, dass die Häufigkeit in der Helgoländer Bucht gegen die an der holländischen Küste nur eine geringe war. Das würde aber nichts an der Tatsache ändern, dass das Verhältnis zwischen „guten" und „schlechten" Jahren bei Helgoland offenbar ein anderes als bei Katwijk sein kann. Es scheint mir nicht unmöglich, dass Helgoland in bestimmten Jahren wirklich sehr viele *Rhizostoma*s hat, nämlich dann, wenn durch hohe Sommertemperaturen die Deutsche Bucht selbst sehr viele Quallen liefern würde. Katwijk hängt aber vom „Süden" ab. Da mag in solchen heissen Sommern die Temperatur durch Einfluss des Kanalwassers etwas niedriger bleiben, auch mögen da die Faktoren, die das Erwachsen der Quallen beeinflussen, weniger günstig als in der warmen Helgoländer Bucht sein. In der Weise könnte Katwijk ärmer an Quallen sein als Helgoland.

Womit die verschiedene Häufigkeit der *Rhizostoma* in Katwijk in verschiedenen Jahren zusammenhängt, kann ich nicht sagen. Theoretisch müssen die Jahre die günstigsten sein, die günstige Verhältnisse während der Strobilations- und Ephyrenbildungsperiode zeigen, das wäre u.a. eine hohe Temperatur im März oder im April bis in den Juni. Diese kommt vor (Fig. 2) in den Jahren '33 und '37. Das stimmt also schlecht; denn *Rhizostoma* war bei Katwijk zahlreich im Jahre 1936 und besonders 1937. Das Heranwachsen der Jungen wird aber von vielen Faktoren beeinflusst, an erster Stelle von der Anwesenheit von Nahrung und Feinden. Was besonders die letzteren betrifft, so ist es sehr wohl möglich, dass eine grosse Häufigkeit anderer Quallen die Zahl der Rhizostomen, die immer später als sie kommen, sehr stark verringert. Besonders die Wahrnehmungen von Fräulein Delap haben gezeigt, wie wichtig Coelenteraten als Nahrung für junge Medusen sind. Wir wissen hiervon aber viel zu wenig, dass wir über diese Sachen mit Frucht urteilen könnten.

6. *General conclusions*

This chapter, because of its numerous small facts, badly needs some general conclusions.

Looking broadly at the distribution and periodicity of the five species studied it is of interest that the medusae with more southerly distribution appear later in the season than those which are distributed farther to the North. This follows best from the following facts:

Cyanea lamarckii Pér. & Les. inhabits the Englisch Channel, the southern and eastern North Sea up to and inclusive the Danish Westcoast and, as *palmstruchii* (Swartz), the Skagerrak. As an exception it is found in the Kattegat till Anholt, Sjelland and even the Kögebugt south of the Öresund. It is especially numerous along the Dutch and German coast. – Its medusae on the Dutch coast occur in greatest numbers from the end of May to the beginning of August.

Cyanea capillata (L.), of which *C. arctica* Pér. & Les., which reaches far to the North, is probably a synonym, is distributed from the English Channel to Norway and the Baltic. Its occurrence in the Channel is rare and may be somewhat doubtful, it is neither numerous nor rare along the Dutch coast, but increases in numbers towards the North. It is common along the Norwegian coast and in the waters between Sweden and Den-mark, and also inhabits the greater part of the Baltic. – Where both *Cyanea* species live side by side, as is the case along the Dutch, German and Swedish coast, the medusae of *capillata* appear and disappear somewhat later than those of *lamarckii* and not earlier as one would expect from their more northern occurrence.

Aurellia aurita (L.) has a worldwide distribution. It inhabits the continental seas of all oceans between 40° S and 70° N, it therefore reaches much farther south than both *Cyanea*s, but it also occurs farther north and east than *C. lamarckii*, as in the Baltic it even reaches the coast of Finland and it occurs along the greater part of the Norwegian coast. – On the Dutch coast the medusae are most numerous from the middle of May to the middle of July, as a rule somewhat earlier than those of *Cyanea lamarckii*.

Chrysaora hysoscella (L.) has its relatives in the South. In Europe it inhabits, besides the Mediterranean, the Atlantic coast of France and the coast of southern England (in the West north to Liverpool and probably – though quite exceptionally – Norway) and the southern North Sea up to the Danish coast. It goes farther north in some years than in others. – Its medusae along the Dutch coast especially occur from August to October, much later than those of the foregoing species.

Rhizostoma pulmo (Macri) also has only southern relatives. It inhabits, besides the Mediterranean, the Atlantic coasts of Europe northward to the Firth of Clyde and the Danish coast, where its occurrence is irregular. – Its medusae along the Dutch coast reach their greatest numbers in September and October.

We thus see that those two medusae, which have the most southerly distribution, occur later in the year than the three more northern ones. The same rule holds good for the Hydromedusae, compare especially the instructive table given by KRAMP (1927, table 15). It is probably a well established fact for several other animal groups; at least the fishes contain striking instances, compare especially RUSSELL (1935).

The pronounced periodicity of the medusae of the different species must have connection with the periodicity in the strobilation period of their scyphistoma's, as it takes a certain time to produce mature medusae from ephyrae. There is, indeed, a similar difference in the period of appearance of the ephyrae as there is between the different medusae. On the Dutch coast the ephyrae of *C. lamarckii* are probably developed from December to June, those of *C. capillata* from March to June, those of *Aurellia* from February to June, but those of *Chrysaora* from the beginning of April (perhaps somewhat earlier) till September, and those of *Rhizostoma* probably from May to September.

The fact that the two southern species propagate so much later in the year than the more northern ones, together with the striking shifting of the time of reproduction northward, may point to the dependence of the periodicity on light or temperature. From what is known on the influence of light on periodicity in general – especially on the important phenomenon of south to north migrations (and vice versa) in birds (ROWAN, 1938) – one would assume that light might be most important here, but the observations make it probable that the chief factor governing the periodicity is the temperature. The evidence for this is insufficient to put it beyond doubt, so that special observations are needed; but there is much in favour of the view that there is a more or less direct influence of temperature on the strobilation period.

For this reason I have tried to put together all such facts as are of interest in connection with the ecological wants of the different stages of the five species studied: scyphistoma, ephyra and medusa. I regret that little attention was given to the planulae, not only by the literature on the subject, but still more by me: a closer study of the wants of the planulae of the different species, including their reactions during attachment, would certainly be worth while.

Scyphistoma

Next to nothing is known about the ecological wants of the polyp stage of the five species studied. As far as I have been able to make out that of *Cyanea lamarckii* has never been found except in the aquarium and the polyps of *Chrysaora* and *Rhizostoma* have at least not been found in the North Sea. Those of *Aurellia* are best known, *Aurellia* being an estuarine form, the polyps of which are numerous in very shallow water. They have been found in large numbers on the coast of the isle of Man, near Plymouth, in Mariager Fjord (eastern Jutland), near Hel (Poland) and on the Finnish coast. They also make their appearance in aquarium tanks and do well in aquaria generally.

As to the depth of their occurrence, it has been assumed by DAMAS and others that the scyphistomas of *Cyanea* are bound to the coast. Bigelow makes it probable, however, that those of *C. arctica*, which is probably the same species as *C. capillata*, occur to a depth of 70 m. The polyps of *Aurellia aurita*, on the other hand, are found in very shallow water (1–2 m in Mariager Fjord, see Ussing, 4–5 m on the Finnish coast, compare Wikström, 1932), probably always less than 20 m or so (Bigelow), but depth figures have several times been omitted from the records (Plymouth, Port Erin).

It is probable that the structure of the bottom is of much importance in so far all scyphopolyps probably need a firm substratum. According to Kramp *C. capillata* is found on stones, shells and algae. Moore, Ussing and Wikström (1932) mention shells (living *Mytilus*, *Pecten*) for *Aurellia aurita*; large numbers, up to ca 100, may occur on one single *Mytilus*-shell (Ussing).

One of the factors interesting us most of all in connection with the annual periodicity is the temperature.

As to the influence of low temperatures *C. lamarckii* must be able to withstand very low ones, possibly below zero, as young medusae on the Dutch coast make their first appearance in February, probably after having been produced from December onward by scyphistomas living in the immediate neighbourhood of the coast. The same may hold for *C. capillata*, though it may have to withstand not such very low temperatures, where it occurs in somewhat deeper water. *Aurellia aurita* lives in shallow water even on the Finnish coast, where the temperature certainly reaches below zero in winter. Judging from the production of young medusae of *Chrysaora hysoscella* near Heligoland in 1925 and other years its scyphistomas must be able to bear a temperature of about 5° C, but this is probably very near the minimum reached. According to Chuin the temperature should not fall below 10° to enable this species to accomplish its „évolution habituelle"; „ce sont surtout le bourgeonnement et la strobilation qui sont compromis, bien que les animaux puissent résister à une variation plus grande de température". *Rhizostoma* must be able to bear temperatures of below 5° C in the polyp stage, for the temperature in January and February 1933 (the year in which *Rhizostoma* was common) was around normal near the Dutch coast and in the German Bight, which means that it must have been in the neighbourhood of 3–4° slightly above the bottom.

Still less is known about the highest temperatures withstood. The distribution of both *Cyanea* species does not reach far south and it is therefore improbable that the polyps can bear high temperatures, but this is uncertain, as it may also be the period of strobilation which limits the distribution. *Aurellia aurita* polyps according to *Halisch* may well bear temperatures of above 20° and this is what one would expect from their distribution. CHUIN says that the scyphistomae of *Chrysaora* find conditions favourable between 10 and 20° C, though they bear higher temperatures, see above. About the same may hold for *Rhizostoma*.

Nothing is known about the influence of salinity on the different polyps except for the fact that *Aurellia* bears a very wide range, compare the remarks by HALISCH on p. 401 of this paper. On the Finnish Coast *Aurellia* lives in a salinity as low as 5.5–6.5$^0/_{00}$, in Mariager Fiord (eastern Jutland) of 14–15$^0/_{00}$. I assume that it may occur in salinities of above 30$^0/_{00}$ quite as well, however; HALISCH kept it in strongly evaporated sea water. – Probably none of the other species bears such a wide range, but *Cyanea capillata* also lives up to far into the Baltic.

According to HALISCH the polyps of *Aurellia* bear great variations in the intensity of illumination. Direct sunshine had no deleterious effect on them. CHUIN states that the scyphistomas of *Chrysaora* do not like the light and were always kept in the shadow.

From the occurrence of *Aurellia* polyps in shallow coastal water we may conclude that they can well bear the influence of silt, but, again, nothing in this respect is known for certain. Neither is there anything known about the influence of water movements.

Strobilation

Strobilation is here meant to include the development of ephyrae, which in nature is, of course, easier to follow than strobilation itself. In connection with it temperature is apparently of prime importance. Nothing can be said about the influence of other factors on the process of strobilation.

Strobilation in *Cyanea lamarckii* on the Dutch coast must start in December. Ephyrae are especially developed from February to April. This means that strobilation proceeds during the coldest part of the year, especially when the temperature may have fallen below 8° and in very cold winters during part of the time to nearly zero. In fact, during the very cold winter 1941–'42 VAN DER MAADEN found a young medusa of *lamarckii* in February, which must have lived as an ephyra in water of below zero in December–January. The production of ephyrae stops in June or earlier, possibly at a temperature somewhere between 10 and 13°. – Strobilation in *C. capillata* starts later in the year and the temperature needed for strobilation by this species may therefore be somewhat higher. It is of interest that in Danish waters according to KRAMP ephyrae may be formed throughout the summer, with a new maximum in autumn. This shows that the summer temperatures in these waters fall within the temperature range of strobilation and that the latter therefore must lie fairly high. – As to *Aurellia* HAGMEIER comes to the conclusion that above 10° C stolonisation is of importance, whereas below 9–10° strobilation begins. The temperature of the sea water during the period in which the ephyrae are formed in NW-Europe is about 4–11° C, which is at least not in contradiction to HAGMEIER's view. Further, the observations of VAN DER MAADEN point to the possibility that there is some connection between the number of *Aurellia* produced within a certain period and the temperature of the water, low temperatures (of 3–4° C) presumably being favourable to the species. This is also shown by CLEVE's data (HAGMEIER, 1930), according to which the ephyrae thrive at 5°, but do no longer feed at 3°. – In the neighbourhood of Bergen (Norway) ephyrae have not only been found in spring, but also in September. This may mean that a double period of strobilation may exist there at least in certain years, a phenomenon comparable to that just mentioned for *capillata*. It may also exist in Holland, see the foot note on p. 398.

Strobilation in *Chrysaora* and *Rhizostoma* on the Dutch coast starts later than that of the preceding species, that of *Chrysaora* in the beginning of April (or earlier), that of *Rhizostoma* probably in May. In both species the period of strobilation continues till about September, but in 1933 and '34, years exceptional for their long and warm summer, the formation of ephyrae must have continued at its least one month longer than in the other years, as medusae of *Chrysaora* were to be found till the beginning of December instead of the end of October, whereas medusae of *Rhizostoma* were to be found till the third decade of November instead of the end of October. November was about normal in '33, somewhat too warm in '34, December was far below normal in '33, far above in '34, so that direct influence of the temperature on the medusae themselves cannot have played a rôle. These facts show that temperature apparently directly influences the length of the strobilation period. The temperature limits of the latter may be 7–20° for *Chrysaora*, 9–20° for *Rhizostoma*, but these figures are rather arbitrary. CHUIN's observations for *Chrysaora*, according to which the temperature for strobilation and stolonisation should lie between 10 and 20° C, are probably not right in so far the lower limit is concerned, as field observations point to an earlier beginning of strobilation, at least in the North Sea; it may begin at a higher temperature on the French coast, however.

As all observations point to the fact that temperature influences the strobilation period I conclude that temperature has more influence on the strobilation than light, contrary to what I had originally expected. One may ask why of the two factors, light and temperature, the first is apparently of greater influence in periodicity phenomena in birds and presumably other vertebrates (ROWAN, and others), the latter in these medusae. VAN REGTEREN ALTENA suggests the possibility to me that light may have become more important in connection with periodicity in bird behaviour because of its great influence on an important activity as the collecting of food, whereas in medusae temperature may be more important, because their food capture is independent from light. Furthermore, temperature generally has more influence on the activities of such lower forms than on those of birds, and this may have played a part too. – It is quite interesting that two different factors may be used for regulating seasonal movements in different animal groups. In fishes, however, both factors may be important, as there are indications that the periodicity of reproduction is influenced by light and that temperature regulates migration data to a great extent.

The strobilation period of a cold loving species like *C. lamarckii* is shorter in the Channel than in the North Sea, presumably because in the South the temperature sinks only for a short time below the upper limit necessary for strobilation. The period of a warmth loving species like *Chrysaora* and *Rhizostoma* is shorter in the North than in the South, because temperatures sufficiently high for strobilation of these species occur in the North for a short period only.

Medusa stage

Temperature does not only influence the *formation* of medusae, but also the time of their appearance in the surface water. In *Cyanea lamarckii* and *capillata* and in *Aurellia aurita*, and to a less degree in *Chrysaora*, the first medusae to appear in spring or early summer are not exclusively young, as one would expect, but of all ages, ranging from one to three or four months. The reason probably is that the young medusae attach themselves to the bottom as long as the temperature is not high enough for them, at least some aquarium observations point in that direction. For *Cyanea lamarckii* there is a more or less distinct correlation between the appearance of medusae at the surface and a rise in the water temperature. The observations for *C. capillata* are too scanty to prove some such connection. For *Aurellia aurita* nothing of such a correlation can be shown to exist, as this species is apparently especially numerous near the surface on days with northern winds and not in periods of warm weather, as is the case with *Cyanea lamarckii*. It therefore looks as if a fall in the temperature, after the latter has risen above a certain level, is necessary to bring the medusae to the surface, a fact difficult to understand. – *Chrysaora*, again, probably comes to the surface as a reaction on temperature rise. For *Rhizostoma* no conclusive observations exist.

This period of apparent bottom life of the young medusae is of very wide distribution, as it has been observed in Europe as well as in North America. It does not occur over the whole range of distribution of the species in question, however, for in Europe it is missing in *Cyanea lamarckii* near Plymouth, *Chrysaora hysoscella* near Valencia Harbour (Ireland) and probably also in *Aurellia aurita* near Port Erin (Isle of Man). It is probably also missing in *Rhizostoma pulmo* near Den Helder, at least in certain years. In North America it is missing in *Cyanea arctica* (probably the same species as *capillata*) near Woods Hole, though it is of much evidence in the Gulf of Maine. There seems little doubt that the degree of latitude has to do with the matter, which may play a part in the following way. Strobilation can start at much lower temperatures than are necessary for the coming to the surface of the medusae. Where really low temperatures are missing the difference between the temperature at which strobilation takes place and the temperature at which the medusae make their appearance is so small, that the medusae can appear soon after development.

It was stated above already that the periodicity in the strobilation period and in the appearance of the medusae shows retardation with the latitude northward. This is especially striking in *Cyanea capillata* and *Aurellia aurita*, the mature medusae

of which may occur till deep into the winter in the northern part of their area of distribution, though they have never been found in winter in the southern part. This occurrence of medusae so late in winter is the natural consequence of the general retardation of the temperature cycle northward. The medusae appear later there, they therefore disappear later too. It is more or less certain that the medusae wich occur so late in the year are those which have been born latest in autumn.

It should be added that the influence of factors on the actual movements of the medusae is dealt with in chapter V of this paper.

When we look at the annual life cycle of these species of Scyphozoa as a whole it is interesting that the cycle is regulated so to speak by the temperature which causes strobilation. It causes the polyp to produce ephyrae, which develop into medusae and mature. The medusae, again, produce planulae and the latter scyphistomas, but the only stage in which we find a certain period of rest is that of the polyp awaiting conditions favourable for strobilation. This is the more interesting, because the stage most susceptible to influences from without, and in the case of our species most in want of the higher summer temperatures, is the mature medusa. The periodicity of its appearance in summer is governed by the periodicity of the temperature which causes strobilation of the polyp stage some 3 months earlier.

IV. DER PASSIVE TRANSPORT

Wir haben uns bis jetzt bei all unseren Gedankengängen benommen, alsob das Wasser stationär wäre und die Quallen nicht vom Fleck kämen. Nur bei der Behandlung von *Chrysaora* und *Rhizostoma* kamen wir für die ersten bei Katwijk angeschwemmten Tiere ohne einen ihrer Erscheinungszeit vorangegangenen Transport nicht aus, für den Rest aber liessen wir eine Verfrachtung ganz ausser Acht.

Da die Eigenbewegung der Quallen im Verhältnis zur Stromstärke sehr gering ist, versteht es sich dass die Tiere, wenigstens solange sie sich im freien Wasser aufhalten, genau wie andere Planktonorganismen die Bewegungen des Wassers mitmachen und so von diesem hin und her geführt und auch ausserhalb des Gebiets, wo sie entstanden, verbreitet werden. Schon ÖSTERGREN (1909) wies mit Nachdruck auf den grossen Wert gerade der

Quallen für das Studium des Planktontransports hin und verschiedene andere Beiträge enthalten Angaben oder Annahmen über einen solchen Transport, die aber wohl stets zu ungenau sind um präzisen Aufschluss über die betreffenden Entfernungen zu geben. Dennoch wäre es von grossem Wert letztere genauer zu kennen.

Wo die Tiere ihre Entfernung senkrecht auf die Küste vergrössern, können wir die Vergrösserung messen, wir wissen diesenfalls aber nicht, in wie weit zugleicherzeit Transport längs der Küste stattgefunden hat; ausserdem sind die betreffenden Entfernungen meistens gering, wodurch das Ergebnis von wenig Bedeutung ist. DAMAS (1909) beschreibt die allmähliche Verbreitung der *Cyanea capillata* an der Küste Norwegens im Laufe des Sommers. "The fact that the jellyfish is an organism of considerable size . . . . and that it keeps near the surface and is therefore easy to observe, and that moreover it is developed near the shore makes it one of the most characteristic organisms in the coastwater. The time of its occurrence in the open sea at the different latitudes and its gradual distribution are clear proof of its vast diffusion and of its passive wanderings. At the period when it has its greatest distribution, in the months of August and September, it extends from the coast to more than 250 miles out to sea, and from the North Sea to Spitsbergen." Diese Beschreibung erregt den Eindruck, dass die Quallen direkt von der Nordsee nach Spitsbergen geführt würden, was, wie wir unten sehen werden, unmöglich ist. Die Tiere würden dabei aber zugleicherzeit 450 km von der Küste hinweg „diffundieren" und wenn die Angabe, dass sie nur in unmittelbarer Nähe der Küste geboren werden, richtig ist, so steht in diesem Fall fest, dass eine Strecke von mindestens 450 km zurückgelegt wurde. Wieviel grösser die Entfernung eventuell sein mag, wissen wir aber nicht, da die Tiere vermutlich nicht senkrecht von der Küste weggeführt werden. – BIGELOW (1928, p. 359-360 und 363) gibt ähnliche Wahrnehmungen für *Cyanea capillata* und *Aurellia aurita* an der amerikanischen Ostküste, die aber etwas ganz anderes besagen. Zunächst ist wichtig, dass er aus der Verbreitung der jungen Tiere zum Schluss kommt, dass die *Cyanea*-Meduse nicht nur in unmittelbarer Nähe des Landes in sehr untiefem Wasser geboren wird, sondern "that this medusa is equally able to pass through its scyphistoma stage in depths of from 30 to 70 meters", während *Aurellia* nach ihm ausschliesslich in sehr untiefem Wasser vorkommt, "probably never deeper than 20 meters or so". Das besagt, dass die Annahme von DAMAS für *Cyanea* unrichtig sein dürfte. Zweitens geht aus den Wahrnehmungen BIGELOWS hervor, dass weder *Cyanea capillata* noch *Aurellia aurita* in der Golf von Maine sehr weit von der Küste wegtreiben. "Cyanea hugs the coast of the Gulf of Maine much more closely than it does the Norwegian coast, where it may drift as much as 250 miles out to sea with the current by September (Damas, 1909). We found Cyanea similarly restricted to the coastal zone within the 100-meter contour from New York southward to Chesapeake Bay during our summer cruises of 1913 (a warm year) and 1916 (a cold year)." "There is nothing in our records to suggest that Cyanea disperses any more widely over the central portion of the gulf in autumn than in summer, and although it is so wide spread in the peripheral zone of the gulf and so plentiful at times near shore, we have never found it in any abundance more than a few miles outside the outer headlands except on the offshore banks as just noted." Und von *Aurellia* sagt BIGELOW dann: "Although Aurelia is so universally plentiful along the coast line of the gulf, it seldom strays more than a few miles offshore. We have only two records of it more than 15 miles from the nearest land, and only more than a mile or two outside the 100-meter contour (fig. 100). Thus its distribution is more strictly coastwise than that of the red jellyfish (Cyanea, p. 357)". Sogar in dem Fall von DAMAS' *Cyanea* also, mag die Angabe falsch sein, weil er wahrscheinlich die Möglichkeit, dass *Cyanea* auch in tieferem Wasser erzeugt werden kann, ausser Acht gelassen hat. Auch fragt man sich, weshalb wohl *Cyanea*, nicht aber *Aurellia* so weit ausserhalb der Küste von Norwegen geraten sollte; über letztere Art spricht DAMAS nämlich nicht. Es wäre aber denkbar, dass die eine Art sich einem solchen Transport widersetzt, die andere Art nicht, vergleiche das nächste Kapitel. Das könnte man auch aus der folgenden Mitteilung von HARGITT (1902, p. 555) schliessen, wenn er das Vorkommen von *Aurellia, Cyanea* und *Dactylometra* bei Woods Hole im Juli und sogar im August beschreibt. "That these were not an isolated few left over from the earlier numbers of April and May is evident in that many were taken in the open waters of Vineyard Sound, and even in the open sea far from land in the region of the Gulf Stream, mostly of the genus Cyanea. They may have been caught up by southward currents from a more northern locality along the coast of Maine or beyond, and carried to these southern ranges." – Eine Angabe über das Hinaustreiben von *Aurellia* wird von ALLEN gemacht, leider aber gibt es nur die kurze Bemerkung in Plymouth Marine Fauna (p. 85): "carried out into the Channel towards the end of the summer".

Sogar diese Fälle einer Beförderung von der Küste hinweg geben also wenig Anhalt für die Berechnung der abgelegten Strecken. Umso weniger werden die Fälle eines Transports der Küste entlang dies tun, wo man mit der Schwierigkeit zu kämpfen hat, dass man nichts sicheres über das Vorkommen der Polypengeneration der betreffenden Tiere weiss.

Es versteht sich, dass die Geschwindigkeit der Wasserströmung bei solchem Transport die Hauptsache bildet. Da der Strom in Küstennähe in der Regel viel mehr an der Küste entlang als von der Küste hinweg gerichtet ist, müssen auch die von den Quallen zurückgelegten Abstände längs der Küste im allgemeinen viel grösser sein als von der Küste hinweg. Es waren besonders die Skandinavier, deren Meeresstudium schon so lange auf grosser Höhe stand, die sich den enormen Einfluss der Meeresströmungen realisierten und dem Transport durch den Strom Rechnung trugen. Zweifellos unter deren Einfluss kam DAMAS zum oben genannten Schluss, dass *Cyanea* direkt von der Nordsee bis nach Spitsbergen transportiert wird. "Born in the spring they have already taken possession of the Skagerack by the month of May, and we find that in this region of the sea all the fry belonging to the three species of the fish we have mentioned (gemeint sind: Schellfisch, Kabeljau und Wittling, deren Jungen Schutz unter die grossen *Cyanea* suchen) have by then repaired to them. This swarm of Medusae, that is swept along by the Baltic current, sees the light of day in the North Sea west of Jylland; and after sojourning for a while in the Skagerack it shapes its course along the coast of Norway on its way to the north. So far as we can discover it receives at all latitudes fresh accessions of individuals that have been born along the coast; since everywhere we encounter young specimens, and everywhere a few of the jellyfish are drawn in towards some place or other on the shore where they die giving the life to their issue" (DAMAS, p. 103). Es sei sogleich darauf hingewiesen, dass DAMAS, wenn stets neue Medusen hinzutreten, natürlich nie beweisen kann, wie lange der Reiseweg jeder ist. Weiter hat er sich nicht realisiert, dass das Wasser ungefähr ein Jahr braucht um von Süd-Norwegen nach den Lofoten zu kommen. – *Cyanea lamarckii* aber (DAMAS, 1909, p. 103–104) scheint auf dem ersten Blick besser zu gebrauchen: "This organism, which is abundant in the Channel, penetrates every summer into the North Sea and Skagerack. It is seldom met with in the deep part of the North Sea outside the 80-meter curve. It rarely advances further than the Skagerack, and it is only exceptionally met with on the west coast of Norway in the latitude of Bergen. Its distribution brings us into contact with the fry of the southern gadoids, *Gadus minutus* (poor-cod), *Gadus luscus* (whitingpouts) and *Gadus pollachius* (pollack)". "In our waters this form and the plankton of which it furnishes the best example are clear proofs of the influence of water that has passed the North Sea. They testify accordingly to the possibility that fry can even come from those southerly regions". Aber auch dieses Beispiel einer langen Reise hält einer Kritik keinen Stand, denn wir haben schon gesehen, dass *lamarckii* sich zahlreich fortpflanzt bei Helgoland, als *palmstruchii* im Skagerrak lebt und, wer weiss, als Scyphistoma an der norwegischen Westküste vorkommen mag. Der Fehler ist also, dass DAMAS die genaue Verbreitung der Polypengeneration oder der jungen Quallen oder die Wachstumsgeschwindigkeit der Medusen nicht kannte oder diese Kenntnisse nicht benutzte. Seine Voraussetzungen sind also auch hier falsch.

Wie schon gesagt waren DAMAS' Auseinandersetzungen seinerzeit nicht neu. Schon AURIVILLIUS (1898 a) nahm für *Chrysaora* und *Rhizostoma* eine Verfrachtung vom Englischen Kanal durch die Nordsee nach der schwedischen Küste an. Ganz auszuschliessen wäre diese Möglichkeit sicher nicht, wir müssen aber bei allen diesen Annahmen eine grössere Vorsicht betrachten als meistens üblich war und tut man das, dann ist ein Transport der *Rhizostoma* vom Englischen Kanal bis zur schwedischen Küste mindestens sehr unwahrscheinlich. Es kommt nämlich, wie wir sahen, ausser der Strömungsgeschwindigkeit des Wassers, ein zweiter Faktor hinzu: die Biologie der betreffenden Stadien. Das galt für *Cyanea capillata* und *C. lamarckii*, das gilt ebenso für *Chrysaora* und *Rhizostoma.*

Wir fanden oben, dass *Chrysaora* und *Rhizostoma* nur in Jahren mit warmem Sommer bis in den November resp. Dezember hinein bei uns vorkommen. Das besagt, wie wir schon sahen, dass die Ursache des späten Verschwindens nicht in der Herbsttemperatur der betreffenden Jahre zu suchen ist, sondern in der hohen Temperatur während der Strobilationsperiode im Sommer. Mit andern Worten, die spät im Herbst noch anwesenden Tiere sind diejenigen, die am spätesten im Sommer geboren wurden; die früh geborenen Tiere sterben schon früher, im Laufe des Sommers. Wir besitzen denn auch keinen einzigen Hinweis, dass die von uns studierten Quallen länger als 4 oder höchstens 5 Monate am Leben bleiben. Nur wenn *Cyanea capillata* und *Aurellia aurita* bis tief in den Winter hinein vorkommen, ist es möglich dass sie älter werden, aber sogar dies ist nicht sicher.

Diese Tatsache, dass der Lebenszyklus der betreffenden Tiere mit in Betracht gezogen werden muss, wurde schon 1900 von Gran betont (Hjort & Gran, 1900, p. 7–8, Gran, 1900, p. 25–26, vergleiche besonders Kramp, 1927, p. 225–227). Nichtsdestoweniger wurde immer wieder dagegen gesündigt, dass man entweder den hydrografischen Verhältnissen oder der Biologie der betreffenden Tiere nicht genügend Rechnung trug. Sogar Kramp (1934), der selbst vor zu weiten Schlüssen warnt, übernimmt von seinen Vorgängern den Gedanken, dass die dänischen Gewässer ihre südlichen Medusen von ausserhalb der Nordsee angeführt bekämen, ohne mit der Möglichkeit zu rechnen, dass sogar diese Reise schon zu weit ist.

Andererseits beweist die relativ grosse Häufigkeit der *Chrysaora* und *Rhizostoma* in den dänischen Gewässern im Jahre 1933 (Kramp, 1934), besonders das Vorkommen der *Rhizostoma* im

Kattegat bis Seeland – wie übrigens genügend bekannt war [1]) – dass diese Medusen weit mitgeführt werden können. Es ist wohl ausgeschlossen, dass sie in diesen Gewässern als Medusen entstehen sollten, dass es im Winter 1933–'34 da also eine Polypengeneration gegeben hätte. KRAMP (1927, p. 235) hat zwar auf die interessante Tatsache hingewiesen, dass bei den Hydrozoa (und gleiches gilt für die Scyphozoa) eine Medusenart in einem bestimmten Jahr indigen sein kann, während sie es ein folgendes Jahr gar nicht ist. Und RUSSELL (1938 a, p. 415) ist diesem Gedankengang noch etwas weiter gefolgt, indem er darauf hinwies, dass eine Polypengeneration unter günstigen Verhältnissen sich irgendwo ansiedeln kann, dann aber in den nächstfolgenden Jahren allmählich verschwinden wird wenn die Verhältnisse wieder ungünstiger sind. Was *Rhizostoma* betrifft, so wollen wir aber annehmen, dass das Vorkommen der Polypengeneration in der Nähe von Skagen ausgeschlossen ist, da diese Art es als Meduse nur selten so weit in nördlicher resp. östlicher Richtung bringt. Es bleibt dann aber die Frage von wie weit her die Tiere denn wohl stammen. KRAMP (1934, p. 212) nimmt, wie AURIVILLIUS, an, dass sie aus dem Englischen Kanal kommen. "*Rhizostoma octopus* is common off the Atlantic coasts of France and in the English Channel, where it is indigenous. Its occurrence off the Belgian coast is very irregular, and most probably it is not indigenous in the North Sea, but is carried in through the Straits of Dover." "The ingoing Channel water with its content of Medusae and other pelagic organisms keeps itself in the middle of the area between the coasts of Belgium, Holland and England, and the resulting current proceeds south of the Dogger Bank towards the west coast of Jutland where it constitutes part of the so-called Jutland Current. *Rhizostoma octopus* belongs to this "Channel water", and as a rule some few specimens are observed off the west coast of Jutland and in the western part of the Limfjord in the autumn, but it rarely proceeds into the Skagerak."

Wenn wir uns nun aber fragen was Stromgeschwindigkeitsmessungen in der Nordsee dazu sagen, dann wird die Sache wenig wahrscheinlich. Wir können dazu zweierlei Angaben benutzen. Erstens Messungen mit dem Strommesser, wie sie auf verschiedenen Feuerschiffen ausgeführt worden sind. Sie haben den Vorteil, dass den Unterschieden in der Wasserversetzung an verschiedenen Stellen Rechnung getragen werden kann und ausserdem ist der Windeinfluss in vielen der Angaben abstrahiert. Zweitens können wir die Resultate der Treibflaschenexperimente benutzen. Diese haben den Nachteil, dass ihr Ergebnis immer mehr oder weniger global ist, ausserdem ist der Windeinfluss nie genau zu schätzen. Für uns haben diese beiden Nachteile aber einen gewissen Vorteil, da es sich erstens um so grosse Entfernungen handelt, zweitens es gerade einen gewissen Wert hat, wenn der Windeinfluss mit zum Ausdruck kommt. Denn Quallen, die sich im Oberflächenwasser aufhalten, werden, genau wie dieses, viel schneller mit dem Wind als gegen denselben mitgeführt werden. Und es kommt für uns auf die grössten Stromgeschwindigkeiten an, da diese bestimmen ob eine Art ein Gebiet erreichen kann oder nicht.

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[1]) Wie schon gesagt wurde in 1873 *Rhizostoma* nach MÖBIUS sogar bei Kiel gefunden (KRAMP 1934, p. 219). Auch das Vorkommen von *Chrysaora* und *Rhizostoma* im Oktober 1896 an der schwedischen Skagerrakküste wurde oben schon genannt.

Im Zusammenhang mit den Treibflaschenmessungen sei aber noch eines hinzugefügt. Die Quallen können sich im Oberflächenwasser aufhalten, tun das aber keineswegs fortwährend. Die Geschwindigkeiten der Oberflächentreibflaschen sind representativ für die oberste Wasserschicht, die vom Wind unmittelbar beeinflusst wird (der ganz oberste Teil der Flasche ist sogar direktem Windeinfluss ausgesetzt). Das Wasser einige Meter unter der Oberfläche (wieviel Meter hängt von der Stärke des Windes ab) steht aber viel weniger unter Windeinfluss als die Oberfläche selbst und die Höchstgeschwindigkeiten der Treibflaschen werden also im allgemeinen für Quallen zu gross sein (1). Am besten wäre es denn auch Verfrachtungsversuche mit etwas unter der Oberfläche hängende Körper (dragbottles) zu benutzen, da diese (vgl. GILSON, 1924 und CARRUTHERS, 1930) nicht so sehr vom Wind beeinflusst werden wie die Oberflächenflaschen und deshalb in ihrer Bewegung etwas besser als letztere den Quallen gleich kommen. Es sind aber nicht solche ausführlichen Einzelheiten über ihren Transport in dem von uns studierten Gebiet bekannt wie für die Oberflächenflaschen. Deshalb werden die Resultate der Experimente mit letzteren hier benutzt. Zugleicher Zeit sei aber darauf hingewiesen, dass die Maximumgeschwindigkeiten für Treibflaschen von den Medusen gewiss nie erreicht werden.

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(1) HARVEY (1928, p. 103) ist der Meinung (und CARRUTHERS, 1930, p. 244, pflichtet ihm hierin bei), dass “the wind-blown surface particles, after travelling a short distance, sink, to be replaced by particles from below, and in this way translocation of water masses with particular characteristics, containing characteristic organisms, does not take place at anything approaching the speed of a floating object”. Danach wäre die Geschwindigkeit von Treibflaschen also sogar grösser als die von Organismen, die sich konstant im Oberflächenwasser aufhalten.

Als Ausgangspunkt sei der ausführliche und wertvolle Beitrag CARRUTHERS' (1925) über die Treibflaschenexperimente in der südlichen Nordsee genommen. Nach diesen Ergebnissen variiert die mittlere Geschwindigkeit in nordöstlicher Richtung der „schnellsten'' Flaschen in den Monaten März bis Oktober von 1.5 bis 2.5 Seemeilen täglich (ausgesetzt von Sandettie Leuchtschiff in der Doverstrasse) und 1.7 bis 4.2 Seemeilen täglich (ausgesetzt von Noordhinder Leuchtschiff in der südlichen Nordsee). Die Geschwindigkeit in ostnordöstlicher Richtung ist etwas grösser, 2.1 bis 3.2 Seemeilen für die Flaschen von Sandettie, 1.8 bis 4.– für die Flaschen von Noordhinder. Das sind alles mittlere Geschwindigkeiten. Die höchsten Geschwindigkeiten für die schnellsten Flaschen in der Periode März-Oktober sind für Sandettie 2.7 (NO) und 3.9 (ONO) und für Noordhinder 5.5 (NO) und 5.7 (einmal 7.1) (ONO). Für Nov.–Februar sind die Werte bisweilen ansehnlich höher, bis maximal 9.7 Seemeilen täglich im Dezember; der Wind spielt dann eine sehr grosse Rolle. Nehmen wir nun als Maximum für NO und ONO Flaschen in der Periode März–Oktober 5.5 Seemeilen täglich und als mittlere Geschwindigkeit 4.– Seemeilen an, dann finden wir, dass die Reise Dover–Skagen – mindestens 480 Seemeilen – für die schnellsten Flaschen mindestens 87, im Mittel 120 Tage dauert. Wir können also sagen, dass die Reise mindestens 3–4 Monate nimmt. Nehmen wir aber – was richtiger ist – eine mittlere Geschwindigkeit für die schnellsten Flaschen von nicht mehr als 3 Seemeilen im Etmal an, so dauert die Reise schon mehr als 5 Monate. Das bedeutet, dass *Rhizostoma*s, die Anfang September bei Skagen gefunden werden, zwischen Anfang Juni und Anfang April südlich von Dover starten müssten. Wenn aber die Temperatur im östlichen Englischen Kanal in den Monaten März bis Mai genügend hoch ist um Ephyren zu liefern, so können sie ab Juni ebenso gut oder besser in der südlichen Nordsee entstehen, es sei denn dass die Wintertemperaturen dort zu niedrig für das Überleben der Scyphistomas sind oder dass die niedrige Salinität ungünstig für sie ist. Letzteres, obgleich wenigstens für bestimmte Jahre nicht wahrscheinlich, wäre nicht auszuschliessen.

Es weisen aber, wie schon gesagt, Funde von Jugendstadien mit Sicherheit auf die Bildung von *Rhizostoma*-Medusen in der südlichen Nordsee hin.

Erstens hat Stiasny (1930) eine Beschreibung von postephyralen Stadien von der belgischen Küste gegeben. Stiasny publiziert nur die Katalognummern dieser Exemplare, nicht Datum und Fundort. Aus einer von Herrn Professor van Straelen gegebenen Auskunft geht aber hervor, dass diese Tiere alle in den Monaten Juni und Juli in unmittelbarer Nähe der belgischen Küste gefangen wurden.

Es handelt sich, so weit es die kleinen Stücke betrifft, um die folgenden Exemplare:

Grösse (mm)	Nummer	Datum	Fundort	Tiefe (m)
5	3077	20. VII. 1904	Querab Oostduinkerke	2.5
5–8 (3 Ex.)	4351	20. VII. 1904	Querab Raversijde	3.5
7	4360	27. VI. 1907	Im Hafen v. Oostende	Oberfläche
8	4337	21. VI. 1907	Im Hafen v. Oostende	Oberfläche
9	4360	27. VI. 1907	Im Hafen v. Oostende	Oberfläche
10	4350	19. VII. 1907	Querab Mariakerke	4.5
11	3076	20. VII. 1904	Querab Oostduinkerke	2.5
12 (2 Ex.)	3077	20. VII. 1904	Querab Oostduinkerke	2.5
13	4350	19. VII. 1907	Querab Mariakerke	4.5

Für die kleinsten dieser Tiere ist es wahrscheinlicher, dass sie an der belgischen Küste geboren wurden, als dass sie aus dem Kanal stammen.

Wie wir schon oben sahen, werden die Medusen auch bei Den Helder geboren. Da erscheinen, wenigstens in bestimmten Jahren, ab Anfang Juli zahlreiche kleine *Rhizostomas*. Solche Tiere bleiben vermutlich, zusammen mit grösseren, in grosser Zahl anwesend bis Ende August oder später. Ein Teil dieser Tiere ist nicht grösser als 1 cm.

Von noch mehr Bedeutung ist, dass auch die Umgebung von Helgoland junge Rhizostomen liefert. Stiasny (1928) hat ein Exemplar von 2.5–3 mm beschrieben, am 23.–26. Juli 1895 bei Helgoland gefunden, 4 Exemplare von 3–18 mm Schirmbreite vom 26. Juli 1922 („Büsumfahrt'' Helgoland) und ein Stück von 18 mm vom 18. August 1924, Cuxhaven. Diese Tiere sind so jung, dass sie unmöglich von südlich von Dover stammen können, denn die Reise Dover–Helgoland (270 Seemeilen) nimmt mindestens 50–70 Tage in Anspruch und Tiere von bis 10 mm Grösse sind wohl nicht älter als einen Monat. – Schliesslich fand KÜNNE (KRAMP, 1934, p. 214–217) im Juli 1925 bei Helgoland "one fairly small specimen", während er 1933 *Rhizostoma* nicht nur schon Ende Juli fand, sondern auch (und zwar im September) "sehr viele in allen Grössen". Dies legt die Vermutung nahe, dass die Tiere im Jahre 1933, dem Jahr ihrer grossen Häufigkeit in den dänischen Gewässern, in grösserer Zahl bei Helgoland geboren wurden.

Es fragt sich sogar, ob *Rhizostoma* nicht als Ausnahme noch nördlicher als Meduse entstehen kann. Es wurde oben schon ein Exemplar vom 12. Juli 1916 aus dem Oslofjord erwähnt (KRAMP, 1934, p. 213). Nach dem, was wir über die Zeit des Erscheinens in der südlichen Nordsee hörten, scheint es sehr unwahrscheinlich, ich möchte sagen ganz und gar unmöglich, dass das Tier aus Oslofjord schon so früh im Jahr aus der südlichen Nordsee angeführt sein könnte. Oslofjord mag im Herbst, nach den Beobachtungen von COLLETT (1905, p. 38–39), von nicht wenig Sardellen (*Engraulis encrasicholus* Cuvier) besucht werden und auch ein reifes Weibchen dieser Art aus dem Mai ist von dort bekannt. Auch andere südlichen Fischarten wurden da mehrmals gefunden, so ist das relativ öftere Vorkommen vom Schwertfisch, *Xiphias gladius* L. (vergleiche COLLETT, 1902, p. 50–53), auffallend, ebenso der Fang eines fliegenden Fisches: *Cypsilurus heterurus* (Rafin. Schmalz) (vergl. BRUUN, 1938), u.s.w. Das besagt, dass der Fjord, wohl durch ihre Wärme, günstig für südliche Tiere ist, und zwar gilt das, nach den Temperaturangaben, für das Oberflächenwasser, vgl. HJORT & GRAN, 1900, table III d. Die genannte *Rhizostoma* könnte also da geboren sein.

Diese Tatsachen nun beweisen, dass die Rhizostomen der dänischen Gewässer nicht von ausserhalb der Nordsee stammen können, sondern in ihr selbst geboren werden. Wir fanden nämlich, dass Tiere, die Anfang September bei Skagen gefunden werden, zwischen Anfang April und Anfang Juni südlich von Dover starten müssen. Es erscheinen aber bei Katwijk keine Rhizostomen aus dem Süden vor dem August, solche Tiere können also nie Anfang September die dänischen Gewässer erreichen. Dagegen entstehen an der belgischen Küste, bei Den Helder und bei Helgoland junge Rhizostomen ab Juni oder Juli. KRAMP findet Rhizostomen bei Hansholm und Hirtshals von Anfang September an. Die Entfernung von Helgoland bis Hirtshals beträgt ungefähr 250 Seemeilen. Bei einer Wasserversetzung von 3–5.5 Seemeilen täglich wird diese Entfernung in 83–45 Tagen zurückgelegt. Die Tiere von Hirtshals können deshalb aus der näheren Umgebung von Helgoland stammen, sicher aber nicht von weiter südlich, wahrscheinlich ist, dass auch weiter nördlich in der Helgoländer Bucht noch Rhizostomen gebildet werden und dass es besonders diese Gebiete sind, die das Innere der dänischen Gewässer mit Rhizostomen versehen. Dazu müssen aber zwei Bedingungen erfüllt werden. Es müssen erstens an den betreffenden Stellen Scyphistomen vorkommen und zweitens müssen die Verhältnisse genügend günstig für Strobilation und das Heranwachsen der Ephyren sein. Das vermutliche Entstehen junger Quallen bei Helgoland im Jahre 1933 beweist wahrscheinlich, dass die Scyphistomen sehr niedrige Temperaturen vertragen können, denn die Temperatur war im Winter 1932–'33 etwas unter normal. Beschränkender Faktor ist also offenbar zunächst die Temperatur in der Periode der Strobilation oder des Heranwachsens der Quallen. Nördlich von Helgoland aber, wo die Medusen nicht jeden Sommer auftreten, beschränkt vermutlich auch das Fehlen der Scyphistomen das Entstehen von Quallen, denn wir dürfen annehmen, dass die Polypen nicht am Leben bleiben, wenn einige Jahre hindurch die Temperatur zu niedrig für die Strobilation bleibt, und es können dann also, auch in einem warmen Sommer, keine jungen Quallen entstehen. Umgekehrt möchte ich annehmen, dass eine Bildung von Ephyren in den Gewässern östlich von Skagen, wenn es zwei heisse Sommer nach einander und einen milden Winter dazwischen gibt, nicht unmöglich sein muss. Auch das Vorkommen von *Rhizostoma* im Sommer im Oslofjord wäre in dieser Weise zu erklären.

Alle die obigen Gedankengänge gelten in der gleichen Weise für die andere südliche Art, *Chrysaora*. Für sie ist es nicht weniger sicher, dass sie in der südöstlichen Nordsee "indigen" ist. Bei Den Helder sind, soweit ich mich ohne Notizen entsinnen kann, kleine Tiere ab Anfang Juli zahlreich. Was Helgoland betrifft, gibt KÜNNE (KRAMP, 1934, p. 214) an, dass im Juli 1925 Quallen aller Grössen, von 8 mm an, gefunden wurden. Solche Tiere sind noch keinen Monat alt und die Reise Dover-Helgoland nimmt, wie wir sahen, ungefähr zwei Monate. Schon KRAMP (1934, p. 214) wies auf die Wichtigkeit der genannten Beobachtungen in dieser Hinsicht hin [1]). Es wurde auch schon die Beobachtung KRAMPS zitiert, nach der junge Tiere ab 3 cm Grösse Ende September und Anfang Oktober 1930 in der Nähe der Kleinen Fischer Bank und von Jutland Rev gefunden wurden (KRAMP, 1934, p. 216–217). Sie kamen ausschliesslich östlich von 6° östlicher Länge vor. Diese Tiere brauchen nicht an der Stelle geboren zu sein, sie könnten z.B. aus der Helgoländer Bucht stammen, es ist aber ausgeschlossen, dass sie ausserhalb der Nordsee geboren wurden, denn Tiere von 3 cm sind höchstens 2 Monate alt und die Reise dauert länger. – Auch die Beobachtungen für *Chrysaora* besagen, wie niedrige Temperaturen die Scyphistomen vertragen können, denn die Wintertemperaturen für die Deutsche Bucht sind die niedrigsten der ganzen Nordsee. Im Winter 1924–'25 waren sie zwar auffallend hoch (GOEDECKE, 1940, Zahlentaf. 3), die Februar-Temperatur muss aber in der Nähe von 5° C gewesen sein. Auch hier muss also die für die Strobilation oder das Heranwachsen der jungen Quallen nötige Temperatur der beschränkende Faktor sein.

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[1]) Merkwürdig genug lässt er drei Jahre später die Möglichkeit, dass sie bei

Wir kommen also zu dem Schluss, dass die Chrysaoren und Rhizostomen, die in den dänischen Gewässern wahrgenommen werden, nicht von ausserhalb der Nordsee stammen, sondern eine kürzere Reise gemacht haben. Gleiches gilt natürlich für *Cyanea lamarckii* aus den dänischen Gewässern, von der KRAMP, wie wir in Kapitel III hörten, annahm, dass sie zum grössten Teil mit der jütischen Strömung aus der südlichen Nordsee angeführt werde. Eine solche kürzere Reise muss aber von allen Tieren dieser Arten gemacht werden und so kommen wir auf den späten Beginn der Periode des Vorkommens bei Katwijk zurück.

Wir fanden, dass *Chrysaora* eigentlich nur ausnahmsweise vor dem August bei Katwijk erscheint. Abgesehen von zwei Junitieren in 5 Jahren, wurde die Art nur im Jahre 1937 im Juli beobachtet, dieses Jahr zwar während einiger Tage in grosser Zahl. Bei Den Helder erscheint *Chrysaora* aber schon Mitte Juni oder jedenfalls Anfang Juli. Die Tiere kommen in Katwijk also einen Monat später als bei Den Helder zur Beobachtung. Wie schon behandelt wurde, nehme ich an, dass sie nach Katwijk aus

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Helgoland geboren werden, offenbar fallen, denn in seiner Bearbeitung der Medusen für Danmarks Fauna (1937) sagt er: „Den er hjemmehørende og meget almindelig i den Engelske Kanal og ved Belgiens Kyst og føres naesten hvert Efteraar med Strømmen til Helgolandsbugten, men optraeder ikke regelmaessigt ved de danske Kyster".

dem Süden angeführt werden. Da sie "im Süden" vielleicht etwas früher geboren werden als bei Den Helder, würde der Transport mindestens einen Monat in Anspruch nehmen. Wenn man nun wiederum mit den obengenannten Treibflaschengeschwindigkeiten rechnet, findet man für die Reise von Dover bis Katwijk – ungefähr 120 Seemeilen – eine Dauer von mindestens 22–40 Tagen, in den meisten Fällen sicher mehr als einen Monat [1]). Es ist also für diese Tiere möglich, dass sie von ausserhalb der Nordsee kommen, aber auch die belgische Küste oder die Gewässer der holländischen Provinz Zeeland könnten sie liefern. Die zwei Juni-Tiere wären dann in der näheren Umgebung von Katwijk geboren. Die Juli-Tiere von 1937, die auffallend gross waren, mögen an einem Küstenteil südlich von Katwijk, aber nicht so weit weg wie die anderen, geboren sein. Ihre auffallende Grösse mag nicht nur mit ihrem Alter (vgl. p. 387 u. 413 dieses Beitrags), sondern auch mit den äusseren Faktoren an dieser anderen Lokalität zusammenhängen.

Auch *Rhizostoma* erscheint bei Katwijk sehr spät, stets im August, offenbar meistens in der 1. Hälfte dieses Monats. Bei Den Helder erscheint die Art schon im Juni oder wenigstens Anfang Juli. Auch sie erscheint also einen Monat später bei Katwijk als bei Den Helder und für sie gilt deshalb genau das gleiche. Mit einem Unterschied aber: dass bei Katwijk nie kleine, junge Tiere beobachtet wurden. Das wäre so zu erklären, dass *Rhizostoma* so schnell wächst, dass sie in ungefähr einem Monat (vielleicht auch etwas mehr) eine ziemliche Grösse erreicht. Das würde bedeuten, dass die an der belgischen Küste, bei Den Helder und bei Helgoland wahrgenommenen Jungen noch jünger wären als wir annahmen, und das wiederum würde die Sicherheit erhöhen, dass diese Tiere nicht von weiter südlich angeführt sein können.

Obgleich *Chrysaora* und *Rhizostoma* in grosser Zahl bei Den Helder geboren werden können, müssen sie die Umgebung auch vom Süden aus erreichen. Die Tiere aber, die Katwijk erreichen in der 1. Hälfte des August, können, unter Berücksichtigung der

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[1]) Die Reise Dover–Hoek van Holland (ungefàhr 100 Seemeilen) dauert mindestens 18–25 Tage, in vielen Fällen sicher mehr als einen Monat. Nur im Winter, bei starken SW Winden, kann diese Strecke bisweilen in 10 Tagen zurückgelegt werden, vgl. CARRUTHERS (1925). Nach ihm beträgt die Geschwindigkeit der Oberflächentreibflaschen ungefähr 1/18 der Windgeschwindigkeit (CARRUTHERS 1930).

Entfernung von 45 Seemeilen, erst 8–15 Tage später bei Den Helder sein, mit andern Worten, Den Helder bekommt wohl keine Quallen von südlich von Katwijk vor dem September.

Rechnen wir jetzt, weil es sich um kleinere Entfernungen an einem Küstenteil, wo gute Strommessungen vorhanden sind, handelt, nicht mit den Resultaten von Treibflaschenexperimenten, sondern mit Strommesserresultaten, dann finden wir für die holländische Küste zwischen den Leuchtschiffen Maas und Haaks (VAN DER STOK, 1905, p. 58), 15–20 km ausserhalb der Küste, eine Wasserversetzung von durchschnittlich [1]) 5.4 bis 6.– km oder 2.9–3.2 Seemeilen täglich. Diese Messungen, bei denen der Windeinfluss eliminiert worden ist, würden ergeben, dass die Medusen die Strecke Katwijk–Den Helder (bis Eingang Westgat: ungefähr 80 km) im Mittel in 14 Tagen zurücklegen. Dieses Resultat stimmt ziemlich gut zu dem obigen. – Nach nicht publizierten Messungen des Rijks Waterstaat beträgt die mittlere Wasserversetzung an der Oberfläche bei IJmuiden 4 km ausserhalb der Küste nur 3.4 km oder 1.8 Seemeilen per Tag. Das ergäbe eine Reisedauer von durchschnittlich 23 Tagen. Die Hafendämme von IJmuiden mögen hier Einfluss ausüben, wahrscheinlich aber ist die Stromgeschwindigkeit näher an der Küste auch kleiner.

Gäbe es also zwischen Katwijk und Den Helder keine Scyphistomen, so wären die bei Den Helder vor dem September beobachteten Medusen von *Chrysaora* und *Rhizostoma* indigen. Es ist aber sehr wohl möglich, dass IJmuiden oder der schwere Seedeich zwischen Camp und Petten solche liefern.

Zuletzt will ich noch auf die Herkunft der Quallen der *Cyanea* und *Aurellia* zurückkommen. Natürlich werden auch sie vom Wasser mitgenommen und über die gleichen Entfernungen wie die anderen Arten mitgeführt. Man möchte nun so gern wissen, ein wie grosser Teil dieser Medusen längs der holländischen Küste mit dem Strom angeführt und welcher Teil da geboren wird. Dies ist leider eine Unmöglichkeit. Es ist aber interessant sich auch hier zu überlegen, was die Wasserbewegung tut. Wenn unsere Annahme richtig ist, dass die Tiere im Frühjahr am Boden bessere Umstände abwarten, kann keine nennenswerte Ortsveränderung stattfinden bevor die Quallen die Oberfläche aufsuchen. Sobald sie letzteres tun, werden sie mit dem Flut- und Ebbwasser vor der Küste nord- und wieder südwärts transportiert, wobei sie täglich im Mittel 5.7 km (sieh oben) nordwärts verschieben. Gibt es nun bald nach der Temperaturerhöhung Seewind, so können sie nur sehr wenig weit mitgeführt worden sein und es werden dann in Katwijk wahrscheinlich Tiere angeschwemmt, deren Scyphistomen vor der Küste lebten. Bleibt

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[1]) Dieses Mittel ist Jahresmittel.

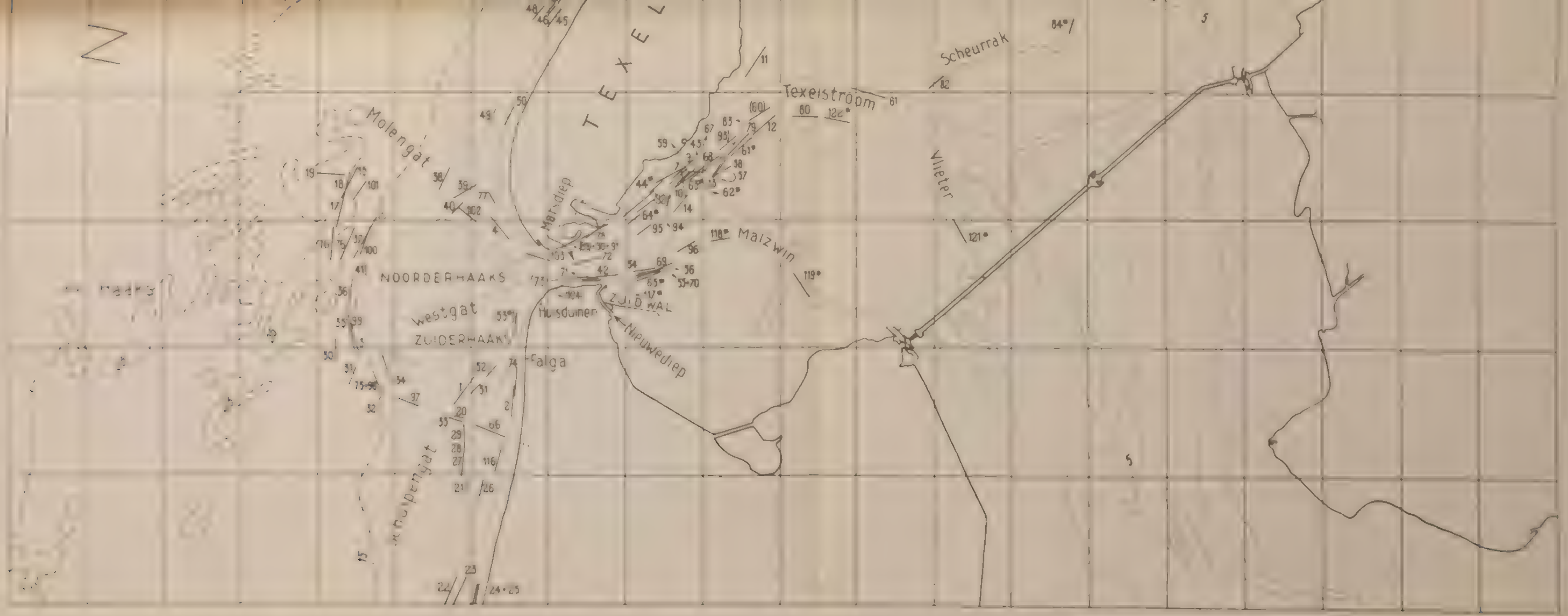
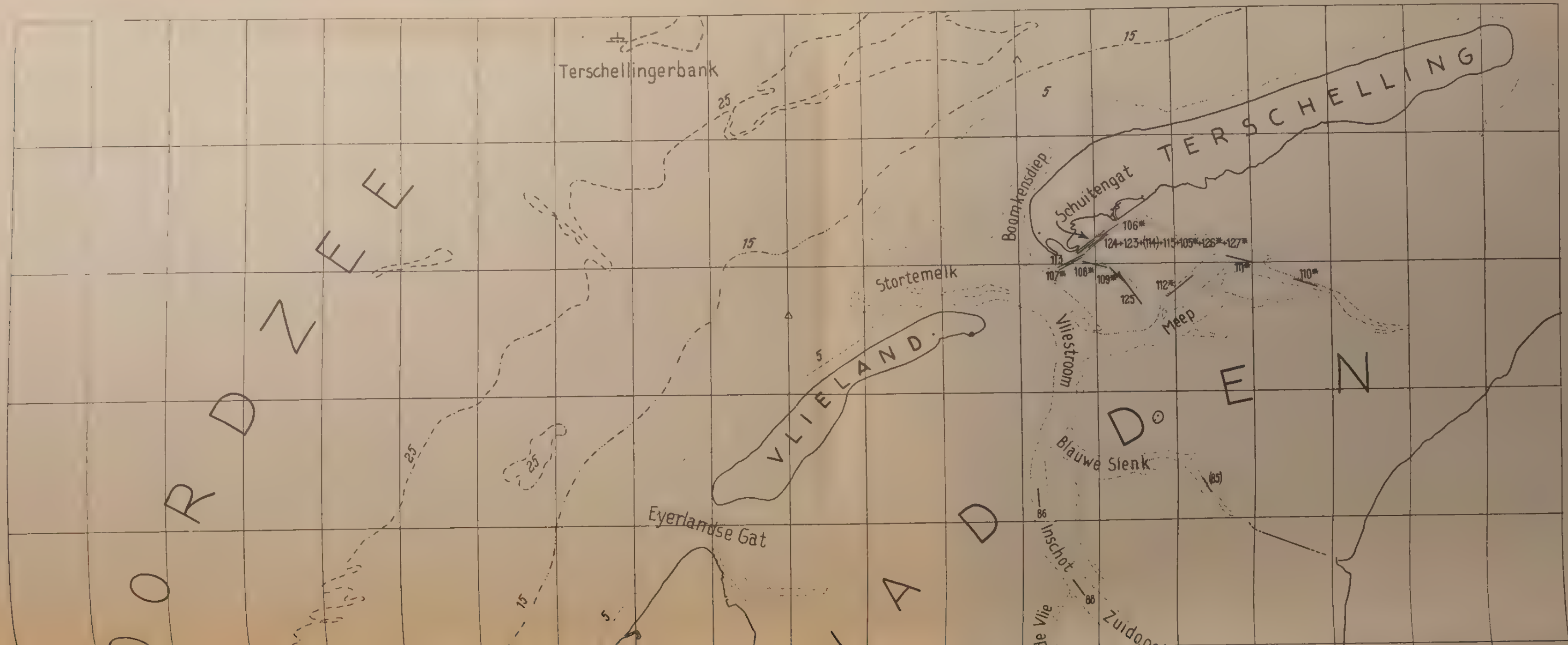


Fig. 1. Karte des von der Zoologischen Station, Den Helder, untersuchten Gebietes (Untersuchungen in den Jahren 1932–1939). Zur Erklärung sieh Text.


Terschellingerbank
25
15
5
TERSCHELLING
Boomkensdiep
Schuitengat
106*
124+123+(114)+115+105*+126*+127*
113
107*
108*
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125
112*
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Stortemelk
Meep
Vliestroom
VLIELAND
ORDZEE
25
25
15
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Eyerlandse Gat
DEN
D
Blauwe Slenk
(85)
86
Inschot
88
de Vlie
Zuidoo
ADD

der Seewind aber längere Zeit aus, so muss Katwijk seine eigenen Medusen grösstenteils abgegeben und andere Medusen aus dem Süden müssen Katwijk erreicht haben. Es müssen dann nach einiger Zeit viele Medusen von südlicheren Küstenstrecken bei Katwijk angeschwemmt werden. Gibt es nun Küstenstrecken, wo weniger Medusen geboren werden als an anderen, dann können die Medusen schwarmweise Katwijk erreichen. Und sind die äusseren Einflüsse an den verschiedenen Küstenstrecken etwas verschieden, so können die Medusen wahrscheinlich auch die Spuren davon in ihrer Farbe oder Grösse mit sich tragen. In dieser Weise entstehen wohl die Unterschiede zwischen verschiedenen „Schwärmen", wie sie von VAN DER MAADEN beschrieben werden. Es gibt hier aber mehr Probleme als Tatsachen und ein schönes Arbeitsfeld wartet auf die Arbeiter.

V. DIE VERTIKALEN BEWEGUNGEN UND DER EINFLUSS ÄUSSERER FAKTOREN

Aus den oben mitgeteilten Wahrnehmungen geht hervor, dass die studierten Medusen regelmässig in geringerer oder grösserer Zahl in Bodennähe vorkommen. Obwohl die Max Weber-Fänge vielleicht einen anderen Eindruck erwecken, ist diese Zahl im allgemeinen klein. Denn wenn das Schiff viele Quallen mit seinem Schleppnetz fängt, sind es deren 600 in einer Viertelstunde. Legt es dabei eine Strecke von 1–2 km zurück und nehmen wir an, dass die Breite der Öffnung des Netzes beim Kurren ungefähr 10 m beträgt, so gibt es höchstens 600 Quallen auf 10.000 m^2 Bodenfläche, inklusive das Wasser dicht über dem Boden, was nur eine Qualle über 17 m^2 ergibt. Das ist also noch sehr wenig. Was aber auffällt ist, dass das eine Mal soviel mehr Quallen unten sind als das andere, und dass bisweilen viele unten sind, wenn es oben fast keine gibt. Obwohl wir im allgemeinen gar nicht wissen, wie die Häufigkeit unten sich zu derjenigen oben verhält, weisen Beobachtungen von Fischern und das Anschwimmen bei ablandigem Wind wohl darauf hin, dass bisweilen relativ grosse Zahlen sich in Bodennähe vorfinden müssen und die von VAN DER MAADEN (1942 b, p. 351) wiedergegebene Beobachtung besagt gleiches.

Auch einige Angaben in der Literatur deuten auf die gleichen Tatsachen hin.

GRAEFFE (1884, p. 341) sagt über das Vorkommen von Quallen im Golfe von Triest: „Die Acalephen sind, wie auch die Hydroid-medusen, besonders an der Meeresoberfläche zu finden, wenn die Nordostwinde reines klares Wasser in der Bucht geschafft haben. Scirocalwetter und Regen sind stets ungünstige Witterung für den Fang dieser und der meisten pelagisch lebenden Thiere, mit Ausnahme der Copepoden welche stets das Meerwasser in allen Schichten erfüllen. Bei solchen Wetterverhältnissen, die eine unreine mit vielem Süsswasser gemengte obere Schichte des Meeres erzeugen, ziehen sich die Acalephen in die Tiefe zurück, wo sie sich an Algen und andere Gegenstände festklammern. Es gelang zuweilen mit dem Schleppnetz, die Thiere hervorzuziehen". Leider wird die Art (es kommen 5 Arten in Betracht) nicht angegeben und auch wird nicht gesagt, woraus gefolgert wird, dass die Tiere sich wirklich am Boden festgesetzt hätten; sie könnten auch einfach am Boden liegen oder ganz dicht über dem Boden im Wasser schweben. – KRUMBACH (1930, p. d 41) macht ähnliche Angaben: „Einzig und allein die Hochsee-Meduse *Pelagia* dürfte sich in allen Formen ihres Daseins ganz auf die oberste Schicht des Meeres beschränken. Von den übrigen Schwimmern mag gelten, was CORI (1928) über die adriatischen Medusen sagt: sie schienen im allgemeinen im tieferen Wasser zu treiben; denn im Inhalte der am Grunde fischenden Schleppnetze fanden sich oft solche Tiere, während sie zu gleicher Zeit in den oberflächlichen Wasserschichten vollständig fehlten". – STIASNY (1921) zitiert VON LENDENFELD, wo dieser sagt, dass *Phyllorhiza punctata* Von Lendenfeld und *Crambessa mosaica* (Quoy & Gaimard) „sich im Winter in der Tiefe, im Sommer vorzüglich an der Oberfläche aufhalten, dass sie jedoch auch während der warmen Jahreszeit in die Tiefe hinabsteigen, wenn das Wetter schlecht und stürmisch ist". „Besonders interessant", sagt STIASNY, „ist eine Bemerkung über die Rhizostomen des Hafens von Sydney (vergleiche VON LENDENFELD, 1884, p. 429): „Nicht allein treiben sie bei jedem Wetter an der Oberfläche (bei Regen zumeist nur kranke Tiere, die nicht mehr tauchen können), sondern sie finden sich auch in solcher Menge am Grunde, dass das ganze Dredgenetz öfters von ihnen derart gefüllt wird, dass man es gar nicht an Bord bringen kann, ohne sich der Gefahr auszusetzen, durch ein Zerreissen desselben alles zu verlieren". Und aus einem anderen Beitrag VON LENDENFELDS (1885, p. 926) geht hervor, dass *Crambessa mosaica* bisweilen mit dem Trawl in 10 bis 20 Meter Tiefe gefangen wurde.

Es kann also kein Zweifel darüber bestehen, dass die Medusen unter bestimmten Umständen in grosser Zahl in unmittelbarer Nähe des Bodens zu finden sind. Die Angabe FRÄNKELS (1925, p. 662, Fussnote), dass „diese Tiere (gemeint ist *Rhizostoma*) im freien Meer stets nur in den oberen Wasserschichten leben und niemals in die Tiefe steigen", ist denn auch unrichtig, sie wird wahrscheinlich, abgesehen von den hier gemachten Angaben, durch Expeditionsfunde oder Faunenlisten schon genügend widerlegt. Übrigens gibt RUSSELL (1928 a, table I, und 1931 c, table I) für *Cyanea lamarckii* genau die Tiefen an, in denen er die Tiere fand, und BIGELOW (1928, p. 360) erwähnt eine Beobachtung, nach der am 23. Juli 1916 kleine *Cyanea capillata* an einer Station im Golf von Maine 30 m tief so zahlreich waren, "that one half hour's haul with the 1-meter net . . . yielded 3 gallons of them". – Was die früh in der Saison geborenen Tiere betrifft, so machten die Beobachtungen es, wie wir sahen, wahrscheinlich, dass diese sich während der ersten Wochen nach ihrer Geburt in grosser Zahl in Bodennähe aufhalten. Für diese gilt also in stark erhöhtem Masse, dass sie nicht stets an der Oberfläche zu finden sind.

Wir kommen also sicher nicht ohne den Schluss aus, dass die Medusen weniger Oberflächentiere sind als im allgemeinen angenommen wird, und es fragt sich wie wir dieses Vorkommen teilweise an der Oberfläche, teilweise tiefer, zu interpretieren haben.

Wenn man über die Lebensweise der Medusen nachsinnt, fühlt man darin sozusagen Inkonsequenzen. Die Hauptsache ist wohl die, dass die Medusen allererst Organismen des freien, offenen Wassers sind, dass sie, trotzdem, gerade längs den Küsten sehr zahlreich vorkommen und demzufolge viel durch Anschwimmen vernichtet werden. Das stimmt nicht. Wenn man nun aber DAMAS' Beschreibung der Verfrachtung von *Cyanea* liest, so fragt man sich, ob gerade dieses Anschwimmen nicht die Verbreitung der Tiere begünstigen könnte, indem es die Planulae in untiefem Wasser freimacht. "These larvae however do not attach themselves and develop unless they find bottom along the coast. Many die on the way. Others escape destruction owing to the circumstance that, when the parent Medusae are thrown mutilated and mangled in numbers upon the shore, they becone liberated and at once fasten themselves to stones and algae" (1909, p. 101). Eine ähnliche Annahme findet man schon bei AGASSIZ (1862, p. 77), dem DAMAS seine Voraussetzungen entnommen haben

mag. Man könnte die Sache also so sehen: Die Medusen bilden das Stadium der Art, das der Verbreitung dient, die Verbreitung ist hier nicht nur, wie bei so vielen festsitzenden Arten, den Larven (Planulae), sondern besonders den Geschlechtstieren, den Medusen, überlassen. Verbreitung durch Verfrachtung aber findet am besten statt, wenn die Wasseroberfläche bewohnt wird. Die Geschlechtstiere müssen also Reaktionen haben, die sie nach oben führen. Die Oberfläche mag aber unter bestimmten Umständen ein ungünstiges Milieu bilden, es wäre also von Vorteil, wenn die Tiere auch im Stande wären die Oberfläche wieder zu verlassen. Ich füge hinzu, dass ich solchen teleologischen Gedankengängen wenig Wert beimesse, sie mögen aber als Einleitung zum Folgenden doch einen gewissen Wert haben.

Fragen wir uns also, wie wir das Vorkommen von Medusen mehr oder weniger abwechselnd an der Oberfläche und tiefer zu verstehen haben, so liegen zwei Annahmen auf der Hand. Die erste ist, dass die Tiere aktiv, die zweite dass sie rein passiv (z.B. Dichteunterschieden wegen), Vertikalbewegungen ausführen.

Eine kurze Durchsicht der Literatur über die Fortbewegungsmöglichkeiten der Medusen zeigt uns, wie wunderliche Gänge die Entwicklung unserer Einsicht in dieser Materie gemacht hat, und zum besseren Begriff von dem, was folgt, möchte ich die Sache kurz referieren.

Anfänglich wurde angenommen, dass die wie Statozysten aussehenden Randkörper der Medusen, wie die Statozysten jedes anderen Tieres, dazu dienen das Gleichgewicht zu bewahren, und dass die Tiere, was auch logisch wäre, sich also im Raum orientieren und gerichtete Bewegungen ausführen können. Dann zeigte VON UEXKÜLL (für die ältere Literatur siehe LEHMANN, 1923, p. 322 ff) für *Rhizostoma pulmo*, dass wir in den Randkörperchen Receptionsorgane für mechanische Reize zu sehen haben „und weiter nichts". Ihre Bewegung sollte die Erregung für die Pulsation liefern. Wir meinten wenigstens, dass er das dargetan hätte. „Der hohle Stiel des Randkörpers mit seinen Concretionen am freien Ende (die Statozyste also) gleicht dem Klöppel einer Glocke". „Bei jedem Schlag (der Meduse) werden die Randkörper hin und her bewegt. Dadurch erzeugen sie eine Erregung, die sich im Nervennetz verbreitet." VON UEXKÜLL betonte, dass *Rhizostoma* Reizen gegenüber ihre Bewegungsrichtung nicht ändern könne, sie werde ausschliesslich von der Form der Tiere bestimmt. Im Zusammenhang damit ist LEHMANNS Aussage, p. 355–357, lesenswert. Während VON UEXKÜLL aber 1901 annahm, dass *Rhizostoma* gar nicht im Stande sei gerichtete Bewegungen auszuführen, schrieb er 1921, dass die Meduse, weil schwerer als das Wasser, dauernd pulsieren müsse, um sich an der Oberfläche zu halten. „Der schwere Stiel sorgt dafür, dass die Richtung „Schirm oben" dauernd erhalten bleibt und nach äusseren Störungen bald wieder eingenommen wird" (p. 62). Letzteres (die Anschauung wurde schon lange von BETHE vertreten, man sehe besonders BETHE, 1910) zeigte auch LEHMANN für *Cyanea* und *Chrysaora*.

Die Erhaltung des Gleichgewichts kommt nach diesem rein mechanisch zu Stande, indem die ruhenden Tiere unten schwerer als oben sind. Dies an sich macht das Vorkommen von Statozysten nach LEHMANN schon unwahrscheinlich, ausserdem aber glaubte er an befestigten sowie freien Tieren feststellen zu können, dass bei den Medusen keinerlei kompensatorische Reflexbewegungen vorhanden sind. Die Randkörper wären nach ihm denn auch nur erregungsliefernde Organe und nicht der Erhaltung des Gleichgewichts dienlich. LEHMANN bestätigte also die Angaben VON UEXKÜLLS. Wenn die Tiere aber fortwährend rein mechanisch in die Vertikallage zurückgleiten, so bleibt von der ungerichteten Fortbewegung nicht viel übrig, da sie schon rein passiv eine Richtung erhalten. Dann hätten sie aber zugleicherzeit nur eine Richtung, nämlich die vertikale. FRÄNKEL (Fussnote, p. 662) wies aber schon darauf hin, dass dem nicht so ist und „dass wir die Rhizostomen im Aquarium wie auch im freien Meere gewöhnlich in einer von der "Normallage" abweichenden Richtung geradlinig schwimmen sehen." In der Tat sehen wir die Quallen, wie auch FRÄNKEL erwähnt, nahe der Oberfläche sehr oft geradlinig horizontal schwimmen.

VON UEXKÜLL betonte, dass die Bewegungsrichtung von *Rhizostoma* ausschliesslich von der Form der Tiere bestimmt werde. In der Tat beschrieb FRÄNKEL, wie die Medusen immer entweder geradlinig oder in gebogenen Bahnen schwimmen und zwar weil einerseits der schwere Stiel, andrerseits die Form der Glocke die Bewegungsrichtung bestimmt. Die Tiere, die ein Defekt haben oder asymmetrisch sind, schwimmen nach ihm in gebogenen Bahnen. Das gleichmässige Pulsieren an sich bewirkt also Geradlinigkeit der Bahn und es ist wahrscheinlich, dass diese Geradlinigkeit für die Medusen von Wert ist, da sie sonst fortwährend korrigieren müssten, sieh unten. Es sei aber sogleich hinzugefügt, dass diese Geradlinigkeit der Bahn mit dem eventuellen „Ungerichtetsein" der Bewegungen natürlich nichts zu schaffen hat.

VON UEXKÜLL und LEHMANN kamen, wie wir sahen, zum Schluss, dass den Medusen Gleichgewichtsorgane fehlen. VON FRISCH (1924) und FRÄNKEL (1925, p. 659 und 681) wiesen aber darauf hin, dass LEHMANNS Versuche nicht beweisend sind, da es sehr wohl möglich ist, dass ein Schwerereiz erst beim Hinzutreten bestimmter äusserer Bedingungen eine gerichtete äussere Einstellung des Organismus auslöst. In der Tat wurde dies von FRÄNKEL bewiesen. Er zeigte für *Cotylorhiza tuberculata* (Macri) (eine Verwandte von *Rhizostoma*) und für *Rhizostoma pulmo*, dass die Randorgane Gleichgewichtsfunktion haben und dass die Tiere fortwährend Kompensationsbewegungen ausführen, die sie in die Normallage zurückführen. Auch Tiere ohne Magenstiel, die also nicht rein mechanisch ihr Gleichgewicht erhalten, nehmen fortwährend die Vertikalstellung ein, die für *Cotylorhiza* (im Gegensatz zu dem, was bei *Rhizostoma* der Fall ist) charakteristisch ist; *Rhizostoma*, die meistens nicht vertikal schwimmt, nimmt nach Abschneiden des Magenstiels die Lage Exumbrella oben ein. FRÄNKEL glaubte aber zu gleicher Zeit, dass an der Erregung liefernden Funktion der Statozysten nicht zu zweifeln sei; sie sollten also auch die rhythmische Pulsation besorgen. Dann aber zeigte BOZLER (1926 a), dass die Rhythmik der Medusenglocke nicht von den Statozysten geliefert wird, sondern bei *Rhizostoma* offenbar vor allem an die Ganglien an der Basis der Randorgane oder (vergleiche 1926 b, p. 800–801) die anderen Teile des Nervensystems gebunden und „autonom" ist. Die

Statozysten haben nach ihm nur Gleichgewichtsfunktion[1]). Aus seiner Beschreibung geht wahrscheinlich auch hervor, dass die Medusen unter bestimmten Umständen geotaktisch reagieren, was VON FRISCH und FRÄNKEL schon für sehr wahrscheinlich hielten. Das geschieht zum Beispiel (p. 45) unter Einfluss von starkem Licht, wobei die Tiere nach unten fliehen. Damit sind wir da angelangt, wo wir anfingen: da wo wir einen Einfluss der Umgebung auf die Schwimmbewegungen der Quallen, von VON UEXKÜLL geleugnet, annehmen dürfen.

BAUER (1927) hat darauf versucht diesen Einfluss der Umgebung auf die Bewegungen und zwar besonders auf die rhythmische Pulsation ökologisch zu verwerten. Sein Beitrag befasst sich hauptsächlich mit der Autonomie der rhythmischen Erregung und dem hemmenden oder fördernden Einfluss verschiedener äusserer Reize auf den Schlagrhythmus, auf den ich weiter unten zurückkomme. – Schliesslich hat HORSTMANN (1934) in zwei Beiträgen eine Zusammenfassung über die Rhythmik und Reaktionen der *Cyanea capillata* und *Aurellia aurita* gegeben. Für uns ist daraus hauptsächlich von Interesse, dass *Aurellia* Lichtreize mit Änderung der Pulsationsfrequenz beantwortet und dass die Lichtperception durch die Pigmentflecke erfolgt. *Cyanea*, die diese Flecke nicht besitzt, hat nach HORSTMANN die Reaktion nicht (vgl. aber die unten zitierten Beobachtungen von DAMAS und ALEXANDER AGASSIZ).

Rekapitulieren wir die Sache ganz kurz, so ergibt sich folgendes. Die von uns studierten Medusen nehmen rein mechanisch eine Vertikalstellung ein, Scheibe oben, Mund unten. Diese muss zum Erfolg haben, dass sie als Folge des ununterbrochenen rhythmischen Pulsierens zur Wasseroberfläche gebracht werden. Dies wird weiter dadurch ermöglicht, dass sie, wenn nicht defekt, geradlinig schwimmen. Unter Einfluss bestimmter Reize können sie ihre Richtung ändern und zum Beispiel horizontal schwimmen. Dabei treten unter Einfluss des Schwerkraftreizes Kompensationsbewegungen auf, die die Tiere in die Vertikalstellung zurückzuführen versuchen. Die Horizontalbewegung wird also das Gleichgewichtsresultat von Schwerkraft- und anderen Reizen repräsentiren, wie das für so viele Tiere unter ähnlichen Umständen gelten soll, vgl. besonders BETHE (1910). FRÄNKEL (p. 678–679) hat diese kontinuierliche Korrektion an einer mit Bleidraht beschwerten *Cotylorhiza* demonstriert.

Der Verlauf dieser physiologischen Untersuchungen führte sehr weit von der Natur fort. Und so hatte man am Ende zu beweisen, dass Tiere ihre Bewegungsrichtung äusseren Reizen zufolge überhaupt ändern können. Es ist denn auch geradezu komisch zu denken, dass eine ganze Gruppe von Forschern, die sich mit der Bewegungsphysiologie der Quallen beschäftigten, das Bestehen der Vertikalbewegungen einfach nicht kannten und den Tieren jede Orientierungsmöglichkeit absprachen, während es daneben einen Russell gab, der, unberührt von diesen Gedanken und mit dem Meere vertraut, die Vertikalbewegungen dieser herrlichen Geschöpfe untersuchte, weil er an ihrer Existenz keinen Moment zweifelte.

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[1]) Interessant ist, dass nach BOZLER (1926 b, p. 802) bei *Pelagia* der wirksame Reiz zur Auslösung von Kompensationserscheinungen der Druck des Randkörpers nach der exumbrellaren Seite, während es bei *Cotylorhiza* (und *Rhizostoma*?) der Druck nach der subumbrellaren Seite ist. Dies würde damit im Zusammenhang stehen, dass *Cotylorhiza* „negativ geotaktisch reagiert", *Pelagia* positiv, sieh unten. HORSTMANN (sieh unten) findet aber bei *Aurellia* und *Cyanea* nicht immer dieselbe Reaktion: bei *Aurellia* war in allen Fällen (mit Ausnahme eines) der Druck des Randkörpers nach der exumbrellaren Seite reizauslösend, bei einem Tier war das Umgekehrte der Fall; bei *Cyanea* zeigte sich keine durchgängige Übereinstimmung. Auch das negativ oder positiv geotaktische „Reagieren" ist nicht konstant, vergleiche unten.

Fragen wir uns zuletzt, was dies Alles im Zusammenhang mit den Vertikalbewegungen der Medusen sagen mag. Dabei sei nicht nur der richtende Einfluss der verschiedenen Milieufaktoren, wovon oben die Rede war, besprochen, sondern auch ihr Einfluss auf die Pulsationsfrequenz, die die vertikalen Bewegungen mit bestimmt. Letztere sollen eben Hauptsache für uns bleiben.

Für die Beantwortung obiger Frage interessiert uns zweifellos das Licht an erster Stelle. Zahlreiche Planktontiere schwanken um ein bestimmtes Lichtoptimum, verschieden nach ihrer Art und eventuell nach der Jahreszeit oder nach Alter und Geschlecht der Tiere, vergleiche besonders die schönen Arbeiten von Russell (an erster Stelle Russell, 1926 b und 1927). Das macht wahrscheinlich, dass auch die Bewegungen der Medusen unter dem Einfluss des Lichtes stehen und dass diese Tiere deshalb nicht nur an der Oberfläche, sondern auch tiefer gefangen werden. Das Bestehen solcher Bewegungen bei den Scyphomedusen ist um so wahrscheinlicher, weil auch eine Anzahl Hydromedusen Vertikalwanderungen abhängig vom Lichte ausführt (vgl. besonders Russell, 1925, '28 a und '31 c), obgleich offenbar, was den Besitz von Lichtsinnesorganen betrifft, ein grosser Unterschied zwischen den Hydro- und Scyphomedusen besteht (Lehmann, p. 362–382). Schon Damas (1909, p. 42–43), wenn er das Zusammenleben von jungen *Gadus merlangus* mit *Cyanea capillata* beschrieb, wies auf den Einfluss täglicher vertikaler Bewegungen der Medusen auf das Vorkommen der Wittlinge hin. Les migrations verticales „sont particulièrement marquées par les jours de ciel clair et paraissent dirigées par un phototropisme accentué. Pendant les heures du jour, les méduses et leurs hôtes sont absents de la surface, on a peine à les découvrir à une dizaine de mètres de profondeur. Elles remontent au crépuscule. Après une journée de calme parfait, durant laquelle il n'a été possible de découvrir aucun signe de vie à la surface, on peut assister, à la tombée de la nuit à un spectacle qui donne une idée de l'abondance des méduses et en conséquence du jeune merlan. Aussi loin que l'oeil peut porter, la mer semble frappée par une pluie abondante et silencieuse. Cet effet est du aux méduses choquant la surface à chaque contraction du disque". BIGELOW (1924, p. 358) schreibt von jungen *Cyanea*: "Alexander Agassiz (1865, p. 45) saw great numbers of them measuring $^1/_4$ to 3 inches in diameter on the surface in Provincetown Harbor in the early morning, all, however, sinking as the sun rose", . . . Weiter sagt BAUER (p. 64), er habe wiederholt beobachten können, „dass bisher unsichtbare *Rhizostoma*- und *Pelagia*-Schwärme bei bedecktem Himmel an die Oberfläche kamen". Auch die oben genannten Beobachtungen von BOZLER an *Rhizostoma* weisen auf das Bestehen von Vertikalbewegungen unter dem Einfluss des Lichtes hin, obgleich sie, beiläufig, an nur zwei Tieren gemacht wurden. Schliesslich weist auch die Tatsache, dass die Pulsation der *Aurellia* nach HORSTMANN vom Licht stimuliert wird, wobei die Pigmentflecke eine Rolle spielen, auf Lichteinfluss hin; seine Beobachtungen sind aber für das Vorkommen draussen nicht leicht zu verwerten.

Einer der wenigen, die gründlich versucht haben, diesen Zusammenhang zwischen der Tiefe des Vorkommens der Planktontiere draussen und der Lichtintensität aufzuklären, ist RUSSELL gewesen. Die Zahl der von ihm gefangenen *Cyanea lamarckii* und *Aurellia aurita* (RUSSELL 1928 a, p. 86) war aber zu klein, um etwas über die Veränderungen ihrer Vertikalverbreitung auszusagen. Und solange keine besseren Beobachtungen vorliegen, können wir die Sache nicht für abgetan halten, besonders wegen der Angaben, die einigermassen gegen einen solchen direkten Einfluss des Lichtes sprechen.

AGASSIZ (vgl. AGASSIZ & MAYER, 1898, p. 5) gibt nämlich für *Dactylometra quinquecirra* (Desor) folgendes an. "It is somewhat strange that almost all of the Medusae which have been observed were found in the brightest sunshine only, or in very dark nights. Early in the morning, and until about ten o' clock, even on clear days, medusae do not make their appearance, while from eleven until one or two o' clock they can be caught in abundance. After this time they disappear gradually, and late in the afternoon it is rare to see a single jelly-fish. Between nine and ten o'clock they come to the surface again; and that hour, in fact, is one of the most favorable for collecting in spite of the darkness". Für *Dactylometra lactea* (Eschscholtz) machen AGASSIZ & MAYER (p. 7) die folgenden Angaben. "The habits of this medusa are remarkable for their extreme regularity; during the morning hours not one of them is to be found, while at about four o' clock in the afternoon they suddenly appear in large numbers, and remain swimming near the surface until long after nightfall." Merkwürdig genug schreibt Mayer (1900, p. 69) genau das gleiche für *Aurellia habanensis* Mayer [= *Aurellia aurita* (L.), vergl. Mayer 1910, p. 623], so genau, dass man sich fragt, ob hier vielleicht ein Irrtum vorliegt: "While in Havana Harbour in February, 1893, we had the opportunity of observing the curious habits of this medusa. During the morning hours not one was to be seen, but at about four o' clock in the afternoon they began to appear in great numbers, and continued to be seen until long after nightfall.". Wie dem auch sei, offenbar machen diese Medusen teilweise aus anderem Grunde als nur des Lichtes wegen vertikale Bewegungen. – Weiter bekommt man von unseren eigenen Medusen den Eindruck, dass sie an sonnigen Tagen eher die Oberfläche als die Tiefe aufsuchen und ähnliches schreiben die Hargitts (1910, p. 220). "So far as we have been able to observe there is no distinguishable influence of light or darkness in the movements of these medusae. We have found them under all conditions of light – early morning, late twilight, the full glare of mid-day sun, indeed so common is Cyanea in this full sun glare that it is commonly designated by fishermen as the "sun scald"." Und Uchida (1926, p. 52) gibt für die Rhizostomide *Mastigias papua* L. Agassiz ähnliches an. "It is to be noted that many ephyrae could be captured at bright noon time, but none at night. This is related to the presence of the yellow cells (Uchida means the zooxanthellae) which are imbedded in the jelly, and a similar case is reported for pelagic actinian larvae of *Zoanthina* by Conklin (1908)." "The adults are also found abundantly at noon time on sunny and calm days. They lie mostly motionless and swim only from time to time in the innermost part of the calm cove where there is no current. When it rains or blows hard, they descend to a greater depth and can not be observed from the surface." – Diese Beobachtungen über ein eventuelles Erscheinen einiger Arten bei Sonnenschein ¹)

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¹) Es sei hinzugefügt, dass Agassiz, der oben im Zusammenhang mit dem Verschwinden junger *Cyanea* bei Sonnenaufgang zitiert wurde, für *Aurellia flavidula* Pér. & Lesueur Angaben macht, die den Wert der für *Cyanea* gemachten Angaben stark herabsetzen. Seine Schlüsse über den Einfluss äusserer Faktoren auf das Vorkommen der Tiere sind ungenügend kritisch (vergl. Agassiz, 1862, p. 76).

stimmen mit unseren in Kapitel III gemachten Angaben über das Erscheinen der *Cyanea* bei warmem Wetter überein. Denn, wie wir wissen, besagten sie, dass es hier wahrscheinlich Zusammenhang mit der Temperatur, nicht mit dem Licht gebe. Dies braucht einem Lichteinfluss nicht zu widersprechen, es bedeutet aber wohl, dass der Temperatureinfluss dem Lichteinfluss unter bestimmten Umständen überlegen ist. Vermutlich liegt die Sache denn auch so, dass Licht und Temperatur beide Einfluss haben, dass die vertikalen Bewegungen vom Licht und von der Temperatur beide verursacht werden, wobei diese einander beeinflussen und die Temperatur oft Überhand haben mag. Damit ist der Fall, ganz allgemein gesprochen, auf ein Beispiel zurückgeführt, wobei ein gewisser Faktor die Abhängigkeit eines Tieres von einem anderen Faktor beeinflusst. In diesem Zusammenhang sind, was Planktontiere betrifft, besonders der wertvolle Beitrag von Rose (1925) und die Angaben von Russell (1926 b, p. 434–436, 1927, p. 252–254) von Interesse.

In der obigen Besprechung des Lichteinflusses wurde unwillkürlich an einen richtenden Einfluss des Lichtes gedacht. Das Licht braucht aber nicht nur einen richtenden Einfluss auszuüben, es ist nicht unwahrscheinlich, dass es durch direkte Stimulation die Pulsationsfrequenz der Tiere und damit die Geschwindigkeit ihrer Bewegungen ändert. In dieser Weise könnten auch die vertikalen Bewegungen beeinflusst werden. Es sind mir aber keine Wahrnehmungen in dieser Richtung bekannt.

Auch die Temperatur hat wohl sicher einen doppelten Einfluss, einen richtenden und einen stimulierenden. – Über den ersten ist mir nichts bekannt, die Annahme liegt auf der Hand, dass die Medusen an Grenzflächen zwischen wärmeren und kühleren Wasserschichten direkt ihre Richtung ändern. So könnten sie bei warmem Wetter, wenn das Oberflächenwasser scharf gegen das kältere Tiefenwasser abgegrenzt ist, oben gehalten werden. – Was den oben erwähnten stimulierenden Einfluss der Temperatur betrifft, so ist längst bekannt, dass die Temperatur die Schlagfrequenz der Medusen ändert. Verlangsamung der Frequenz bei niedriger Temperatur könnte ein Schweben oder Absinken, höhere Frequenz ein Heraufsteigen der Medusen zur Folge haben, was sie auch ohne Lichteinfluss in die Tiefe oder an die Oberfläche bringen könnte. Aus Thills Angaben (1937, p. 60–62) geht aber hervor, dass die Schlagzahl von *Aurellia* aus der Ostsee sich zwischen 9° und 17° kaum ändert, dass Temperaturen unter 9° einen regelmässigen Fall der Schlagzahl verursachen, während auch über 17° die Schlagzahl fällt, erst wenig, dann über 22° schneller. Und obgleich die Dauer der Temperatureinwirkung hier unberücksichtigt bleibt, und wir ausserdem nicht wissen in wie weit ähnliches für die Nordseetiere zutrifft, mag es sein, dass die Art in der Nordsee kaum Pulsationsänderungen als Folge der Temperaturänderungen aufweist, da sie als Meduse fast dauernd zwischen 9 und 17° lebt. Für Aurellien in der Ostsee, die viel niedrigere Temperaturen zu ertragen haben, liegt die Sache aber anders. Auch wo *Aurellia* zeitweise in sehr warmem Wasser lebt, mag es anders aussehen und mag ein Sinken durch Pulsationsabnahme stattfinden. Gleiches könnte für *Cyanea lamarckii* gelten. Was *Rhizostoma* und *Chrysaora* betrifft, kommen ihre Geschlechtstiere im Herbst bei Temperaturen, die gewiss viel zu niedrig für sie sind, bei uns vor. Ein Absinken ihrer Medusen infolge zu langsamer Pulsation mag bei ihnen denn auch regelmässig vorkommen.

Was die Salinität betrifft, so ist wahrscheinlich, dass da, wo plötzliche Salzgehaltssprünge anwesend sind, die Quallen durch diese beeinflusst werden und ihre Schwimmrichtung ändern können, genau wie wir das auch für Grenzflächen zwischen Wassermassen verschiedener Temperaturen annahmen. Es sind mir aber wiederum keine Wahrnehmungen in dieser Richtung bekannt. – Nicht unwahrscheinlich ist weiter, dass zu niedrige Oberflächen- (oder zu hohe Tiefen-) salinität durch Änderung der Pulsationsfrequenz mit einem Sinken (bezw. Aufsteigen) beantwortet wird. Aus Untersuchungen von BETHE (1908) und BENAZZI (1933) geht nämlich hervor, dass Abnahme der Salinität die Frequenz und Intensität der Pulsation bei *Rhizostoma pulmo* und *Cotylorhiza tuberculata* verlangsamt und schliesslich hemmt. BETHE (p. 553), der das Salzwasser mit destilliertem Wasser verdünnte, gibt an, dass bei seinen Versuchstieren (er arbeitete mit *Rhizostoma*) die Schlagfrequenz und -grösse sich innerhalb 48 Stunden nicht änderte wenn die Verdünnung nicht mehr als 20% des Ausgangswertes betrug, darüber hinaus bekam er Verlangsamung und Hemmung. Erhöhung der Salinität ergab unregelmässige Schlagzahl, die aber bald wieder normal wurde. Hinzugefügt sei, dass die Ausgangssalinität hoch war (20.5‰ Cl) und dass bei Erhöhung die Überführung in Aquariumwasser von 22.4‰ Cl stattfand, das dem Seewasser gegenüber Unterschiede gezeigt haben mag. – Weiter beschreibt THILL (p. 75) Erniedrigung der

Schlagzahl für *Aurellia* aus der Ostsee, wenn die Salinität von 7.3 (Ausgangswert) unter 7.–$^0/_{00}$ sank [1]), obgleich die Pulsation zwischen 7.3 und 7.–$^0/_{00}$ erst ein wenig zunahm. Erhöhung der Salinität (von 6.4 oder 7.2 bis 9–17$^0/_{00}$) verursachte (p. 80) höhere Schlagfrequenz. Erniedrigung der Salinität fand mit Leitungswasser, Erhöhung mit konzentriertem Seewasser statt, es wird aber nicht angegeben, wie dieses konzentriert wurde. – Dies Alles weist darauf hin, dass die Tiere bei Erniedrigung der Salinität ihre Schlagzahl verringern und zu Boden sinken werden, dass Erhöhung des Salzgehaltes wahrscheinlich Erhöhung der Schlagzahl und einen Aufstieg verursachen wird. Da nun die Quallen in Wasser von niedriger Salinität ausserdem sinken werden, weil sie spezifisch zu leicht sind, so werden sie, Salinitätsänderungen wegen, in zwei Weisen auf den Boden gelangen: weil sie nicht mehr pulsieren und weil sie spezifisch relativ zu schwer werden. Letztere Möglichkeit kommt weiter unten noch kurz zur Sprache, es sei aber sogleich auf die Wichtigkeit dieser Tatsachen für den Transport der Quallen hingewiesen. Denn in dieser Weise könnte im Küstenwasser dem Transport bis in Gebiete mit einer zu niedrigen Salinität hinein eine Grenze gesetzt sein. Im Wattenmeer z.B. sieht es aus, alsob nur wenig Medusen das Innere erreichten; auch aus dem Übergangsgebiet zur früheren Zuiderzee waren (Redeke, 1922) keine Scyphomedusen bekannt. Der Grund könnte zwar sein, dass wenig Nordseewasser in dieses Gebiet gelangt. Ich glaube aber eher, dass die Quallen es nicht erreichen, wie das auch für viele schwimmende oder halbtreibende Arten gilt, die regelmässig vom Strom mitgeführt werden: Fische, Tintenfische, Schwimmkrabben. Erstere kehren einfach um, wenn der Strom sie in ungünstiges Gebiet führt, letztere graben sich ein um sich wieder vom Strom mitnehmen zu lassen, sobald er kehrt. Quallen nun könnten dasselbe durch Änderung der Pulsationsfrequenz erreichen.

Es sei schliesslich der Einfluss mechanischer Reize besprochen.

Nach Bauer (p. 63–65) tritt auf mehrmalige oder heftige Erschütterung bei frischen, gut erregbaren Tieren unfehlbar eine Hemmung des Schlags ein, die an die Randorgane gebunden ist. Die Pulsation kann dabei sogar längere Zeit zum Stillstand gebracht werden. Diese Beobachtungen scheinen besonders *Cotylo-*

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[1]) Die Salinitätssenkung in diesen Versuchen ging bis 5$^0/_{00}$, *Aurellia* lebt in den inneren Schären von Finnland nach Wikström bis in Wasser von 5.5$^0/_{00}$.

rhiza zu gelten. „Die Arten, welche spezifisch verhältnismässig schwer sind wie *Rhizostoma* und *Pelagia*, sinken alsdann rein passiv in die Tiefe und bleiben, da der Mundstiel mit seinen Filamenten schwerer ist wie die Glocke, stets in dieser Lage, welche sie beim Wiedereinsetzen der Bewegung auch wieder in ihr Wohngebiet, die oberflächlichen Schichten zurückführt". *Cotylorhiza tuberculata* aber verhält sich ganz anders. „Auch diese Art ist spezifisch schwerer als das Wasser, ein Absinken in normaler Lage kommt aber kaum in Frage, da die reichverzweigten Filamente einen zu grossen Formwiderstand bieten, wovon man sich überzeugen kann, wenn man das Tier im Wasser niederzudrücken versucht. Durch den Druck werden die Zweige sofort entfaltet und hemmen nun die weitere Abwärtsbewegung ausserordentlich. So ist es zu erklären, dass sich die Art trotz so häufiger gerade für sie charakteristischer Schlagpausen an der Oberfläche hält. Dauert aber die Ruhe längere Zeit an, wie bei fortwährender Erschütterung etwa durch den Wellenschlag, so tritt eine Änderung im Verhalten ein. Es zeigt sich dann, dass die Schwerkraftsverteilung bei dieser Art eine andere ist wie bei den soeben erwähnten: die Glocke ist schwerer wie die Filamente, ihre massive Mittelpartie stellt geradezu ein zentral wirkendes Gewicht dar, welches zur senkrechten Einstellung in verkehrter Lage führt. In dieser Lage nun kann das Tier leicht absinken, da die glatte, keinen Widerstand bietende Glocke sich über die Kransen des Magenstiels legt. Man kann sich mit der Hand leicht überzeugen, dass mit der Glocke voran die Meduse leicht in die Tiefe geführt werden kann" (p. 65–66). In einer Fussnote fügt BAUER dann hinzu, dass nach BOZLER *Cotylorhiza* sich (auch ohne Kompensationsbewegungen) rein passiv vertikal (Scheibe oben) stellt, ein Widerspruch, den er nicht aufzuklären vermag.

Nicht nur BOZLER, auch FRÄNKEL gibt an, dass *Cotylorhiza* in der Ruhelage den Schirm oben hat und in dieser Lage sinkt. Es mag sein, dass der von BETHE (1910, p. 87–89) genannte Fall von *Solmoneta* (*Aegineta*) *flavescens* (Kölliker) in dieser Kontroverse Auskunft gibt. Er findet, dass diese Meduse ihr spezifisches Gewicht leicht ändern kann und nun, in die verkehrte Lage versetzt, durch Aufrollen oder Umklappen der Tentakeln, die richtige Lage zurückgewinnt. – Was weiter das genannte Absinken der *Rhizostoma* und *Pelagia* betrifft, so beantwortet *Rhizostoma* nach FRÄNKEL (p. 682) jeden mechanischen Reiz (auch das Abschneiden des Magenstiels, wobei dieser also nicht mehr die Gleichgewichtslage verursachen kann) mit Rückdrehung in die Normallage: Schirm oben, um dann (vgl. BOZLER, 1926 a, p. 45) bei Erschütterung und mechanischen Reizen nach oben zu steigen. Das Tier „flüchtet" also diesen Angaben zufolge nicht nach unten (wie BAUER angibt), sondern nach oben. Für *Pelagia* sollte nach Bozler (1926 b, p. 801) das Umgekehrte gelten, was ihm biologisch viel besser verständlich erscheint, da solche Reize wohl nur vom Wellenschlag bei Stürmen ausgehen mögen. Diese Beobachtungen an *Pelagia* widersprechen aber wieder früheren von Bozler (1926 a, p. 46), nach denen auch *Pelagia* nach oben statt nach unten flüchtete.

Ein in die Tiefe Sinken von Medusen im Zusammenhang mit der Wellenbewegung (und ein Wiederauftauchen bei ruhiger See) wird nach Bauer auch von Steuer angegeben; man sehe auch die Angaben von von Lendenfeld (Seite 448 dieses Beitrags), der Hargitts (1910, p. 220), von Lehmann (1923, p. 37 und 380), von Uchida (1926, p. 52, vergl. Seite 455 dieses Beitrags) und Horstmann (1934 a, p. 413) [1]. Aus den Angaben von Lehmann, Bauer und Horstmann geht hervor, dass das Sinken offenbar als Folge verschwindender Reizbarkeit bei Erschütterung stattfindet. Da nun nach Bauer schwache mechanische Reize fördernd, starke hemmend auf den Schlagrhythmus einwirken, so mögen die obengenannten Widersprüche teilweise von der Stärke der Reize verursacht worden sein. Übrigens kann es für ein Tier, das die ganze Wasserschicht vom Boden bis zur Oberfläche bewohnt, von Vorteil sein das eine Mal auf-, das andere abwärts zu „fliehen".

Bauer (p. 50) hat auch den Effekt mechanischer Reize auf bestimmte Teile der Meduse, was ihre Schlagfrequenz betrifft, untersucht. Von diesen Beobachtungen sind für uns besonders die von Interesse, die zeigen, dass bei *Rhizostoma* und *Cotylorhiza* Beschleunigung der Schlagfrequenz auftritt, wenn die Filamente des Mundstiels leise den Boden berühren, während Hemmung des Schlages hervorgerufen wird bei mechanischer Reizung an zahlreichen Punkten zugleich, „wie sie am einfachsten zu erzielen ist, wenn man die Medusen in umgekehrter oder seitlicher Lage an die Wasseroberfläche bringt, so dass ein grosser Teil der Filamente mit der Luft in Berührung kommt." Er wies schon darauf hin, dass die Beschleunigung beim Berühren des Bodens in der Natur von Wert sein mag (p. 67).

Was zuletzt den genannten Einfluss der Wasseroberfläche betrifft, so gibt Fränkel (p. 664) für *Cotylorhiza* an, dass diese Art durch verminderte Schlagfrequenz auf die Nähe der Oberfläche reagiert. Das wird wiederum ein Absinken (oder wenigstens ein Schweben oder geringeres Aufsteigen) zur Folge haben. Besonders die plötzliche Gewichtszunahme beim teilweisen Auftauchen aus dem Wasser mag als Hemmnis auf die Pulsation wirken (Bauer, p. 56–57) und so ein Sinken verursachen.

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[1] Auch für andere Tiergruppen gibt es Angaben über ein Sinken bei stürmischem Wetter, das offenbar bei vielen Planktonformen vorkommt. Korringa (1940) kommt aber, obgleich er selbst angibt (p. 106), dass Austernlarven im Aquarium bei Erschütterung auf den Boden sinken und dort liegen bleiben, zum Schluss, dass sie bei stürmischem Wetter draussen nicht aus dem Oberflächenwasser verschwinden (p. 112).

Die oben referierten Beobachtungen und Experimente machen einigermassen deutlich, in welcher Weise die Medusen zwischen Oberfläche und Boden aufgehängt sind. Das Bild ist zwar sehr unvollständig, wir brauchen aber nicht an dem grossen Einfluss der Umgebung auf die vertikalen Bewegungen zu zweifeln. Licht, Temperatur, Salzgehalt und mechanische oder Erschütterungsreize tun dabei alle das Ihrige.

Daneben aber nahmen wir an, dass auch rein passiv, unter Einfluss von Dichte-Unterschieden, Vertikalbewegungen vorkommen und diese seien also zuletzt noch kurz besprochen.

Die grosse Häufigkeit der Medusen unter bestimmten Umständen in unmittelbarer Nähe des Bodens macht es wahrscheinlich, dass die Medusen nicht nur „aktiv", sondern auch passiv, in Bodennähe gelangen und zwar wenn sie in Wasser von etwas zu niedrigem Salzgehalte zu schwer sind. Schon Vanhöffen (1896) wies auf den grossen Einfluss von Stromkabbelungen – in diesem Fall die Grenzen ozeanischer Wassermassen, wie Golfstrom, Irminger, Ostgrünland, Labrador- und Florida-Strom, andeutend – auf die Schwarmbildung an der Oberfläche hin und 1903 beschrieb er (p. 35) Ansammlungen von Radiolarienkolonien, Velellen, Physalien, Porpiten, Ctenophoren, *Glaucus*, *Janthina* (Gastropoden), Salpen, und besonders Pelagien, alle an den Grenzen dieser Ströme entlang zusammengehäuft. Bigelow (1928, p. 362) schreibt: "it is characteristic of Aurelia to appear suddenly in lines or windrows, often miles in length, as where two tidal currents meet. On such occasions, in calm weather, their shadowy forms can be seen shimmering as far down in the water as the eye can penetrate, while the white genital rings stand out conspicuously on the translucent bodies of those near the surface". Und Russell (1938 b, p. 272) sagt von Medusenschwärmen im allgemeinen: "in many instances such congregations are probably mechanically produced by tiderips, or currents set up by the wind, or where oceanic currents impinge". Schliesslich sei für ein Beispiel auf die oben für Den

Helder genannten Beobachtungen (28. Mai 1933) hingewiesen. – In diesem Zusammenhang ist von Interesse, dass gerade in Landnähe, wo die Medusen so zahlreich sein können, immer Wassermassen verschiedener Dichten auf einander stossen. – Nicht nur die Schwarmbildung an der Oberfläche aber, sondern auch eine Ansammlung am Boden, wird längs solchen Stromgrenzen gefördert werden. Tiere aus Wasser hoher Salinität werden sinken, wo sie mit etwas salzärmerem Wasser in Kontakt kommen, genau wie sie nach der Oberfläche steigen, wo das Umgekehrte der Fall ist. Die Dauer des am Boden Liegens (oder an der Oberfläche Schwimmens) wird von den Dichte-Unterschieden zwischen dem alten und neuen Milieu abhängig sein. Für Medusen kenne ich in diesem Zusammenhang keine Zeitangaben ausser einem von BAUER (p. 57–58) ganz nebenbei gegebenen Beispiel von ungefähr drei Stunden. Das ist aber mehr als genug um bedeutende Anhäufungen zu bilden [1]).

VI. ENGLISH SUMMARY

This paper deals with the periodicity in the occurrence of five species of medusae, which are common along the Dutch coast. Its conclusions are largely based on observations made by H. VAN DER MAADEN, Katwijk aan Zee, Holland, published in the same number of this volume, for a small part on data collected by the author near Den Helder, Holland, and further on data from literature.

The bulk of the material is dealt with in Chapter III. In it the five species are treated separately and the following details are given under each species: 1. the period of occurrence of ephyrae and medusae on the Dutch coast, 2. the same particulars for neighbouring waters, ranging from southern England to the Baltic and Norway, 3. the retardation in the periodicity from S to N, 4. the influence of temperature on the periodicity of strobilation, 5. the life of the medusa preceding its first appearance at the surface, and the influence of temperature upon the latter,

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[1]) Nicht nur die Medusen selbst sind diesen Anhäufungen unterworfen, auch die Rippenqualle *Pleurobrachia pileus* (O. F. Müller) wird bisweilen in so grosser Zahl mit dem engmaschigen Schleppnetz gefischt, dass man wohl eine passive Anhäufung am Boden annehmen muss. Fang nr. 117 vom 27. Juni 1939 (Tabelle I) enthielt ungefähr 30.000 Stück dieser Art. Dabei müssen durch die grossen Maschen im vorderen Teil des Netzes grosse Quantitäten hindurch gegangen sein.

6. the influence of external factors on the numbers of medusae in different years. General conclusions relating to these facts are given (in English) at the end of Chapter III.

Chapter IV deals with the transport of medusae by currents. It is shown that the assumption, *Chrysaora* and *Rhizostoma* are not indigenous in the North Sea, but annually reach the latter (and in some years the Skagerrak and Kattegat) from the South through the Straits of Dover, does not hold, as the medusae of these species are produced within the North Sea and the distances travelled by them in the course of their existence are relatively small only. Of course, all medusae are transported a certain distance and their transport explains the later appearance of *Chrysaora* and *Rhizostoma* at a place where they do not breed than at a place where they breed. It probably also accounts for the appearance of different swarms of medusae of a definite size or colour at certain places. But the distances are relatively short compared with those which were often supposed to occur.

Chapter V deals with the influence of external factors on the movements of medusae, especially on the vertical ones. It is chiefly based on data from literature, which concern the influence of light, temperature, salinity and mechanical stimulation. They combine to present a picture of the way in which the movements of jellyfish are influenced by their surroundings.

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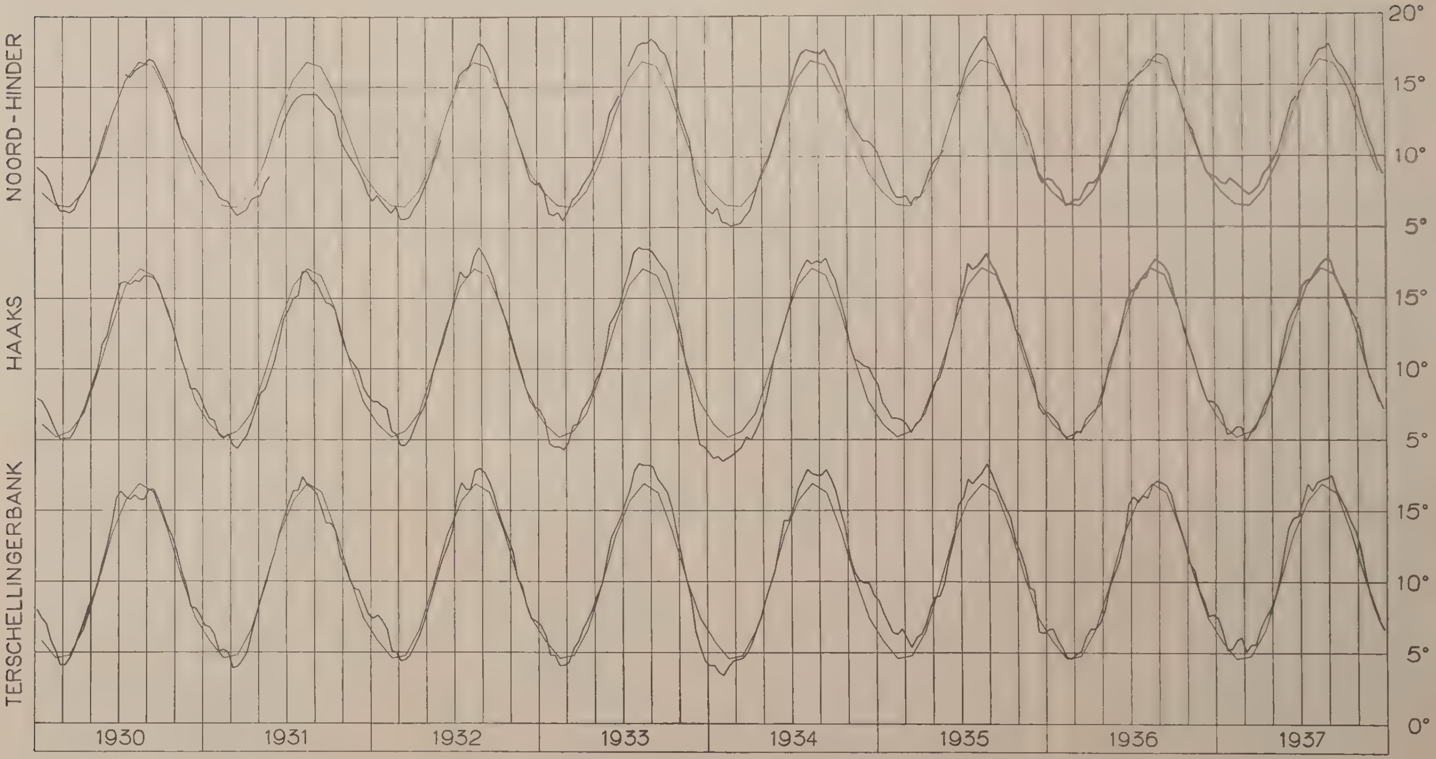


Fig. 2. Temperaturkurven für das Oberflächenwasser in der Nähe der holländischen Feuerschiffe. Dekadenwerte. Dünne Linie: Durchschnittskurve für die Jahre 1921–'37.

COMPTES RENDUS DE LA SOCIÉTÉ NÉERLANDAISE DE ZOOLOGIE

AOÛT 1941 – JUILLET 1942

Séance du 27 septembre 1941 au Jardin Zoologique „Blij-Dorp'' à Rotterdam

1. Introduction du Directeur, M. le Dr. K. Kuiper sur: Dessein et organisation du Jardin Zoologique „Blij-Dorp''.

Le déplacement du Jardin Zoologique de Rotterdam a été sérieusement à l'ordre plusieurs fois.

Le troisième plan seulement pouvait être réalisé. Trois avant-projets d'un nouveau jardin ont été faits.

Le projet exécuté par l'Architecte S. van Ravesteyn a des qualités qu'on ne saurait méconnaître. On y admire en premier lieu le style élégant et joyeux et l'harmonie entre les détails du plan. Quand on se mit à l'ouvrage la situation politique était déjà pleine de menaces, bientôt la guerre fut déclarée. Dans ces circonstances le développement et l'exécution des plans furent tellement pressés qu'on n'a pas toujours fait droit aux demandes de la pratique de l'exploitation.

Les instituts culturels particuliers non-subventionnés rencontrent de grandes difficultés dans leur lutte pour la vie. Pour cette raison l'exploitation du Parc Zoologique Blij-Dorp a été fondée sur certains principes, qui promettent un compte sans déficit. Il n'y a pas de collection zoologique et botanique représentative mais il y a une sélection d'animaux et de plantes, qui peuvent beacoup intéresser le grand public. On s'occupe chaque jour des divers animaux et on les nourrit en public, ce qui offre une distraction convenable et instructive aux spectateurs. Des expositions de fleurs, des concerts, des représentations de ballets contribuent à couvrir l'exploitation du complex „Rivièra-Hal'' avec son café-restaurant soigné.

Le Rivièra-Hal (grande salle, où l'on prétend imiter le climat de la Côte d'Azur) formant un ensemble avec les bâtiments des singes, des pachydermes et des reptiles et avec les serres de plantes, voilà le centre du parc zoologique Blij-Dorp, spécialement pendant les mois d'hiver, la saison morte des autres jardins zoologiques.

L'effort de faire un Zoo visité par le public pendant toute l'année et non seulement pendant l'été semble être un succès jusqu'ici.

Après avoir résumé les allures modernes de l'exploitation du nouveau Parc Zoologique de Rotterdam M. KUIPER indiqua les règles principales pour la construction des logis d'animaux, qui, selon la définition lapidaire d'un collègue allemand, ont pour but: „das Tier in seinem Aussehen und seinem Verhalten zur Geltung zu bringen".

2. Après cette introduction, les membres, au nombre d'environ 50, visitèrent le terrain et les bâtiments sous la direction de M. le Dr. K. KUIPER et Mme le Dr. A. GIJZEN.

Séance du 8 novembre 1941 à Amsterdam

1. P. D. NIEUWKOOP (Utrecht). Quelques nouveaux renseignements sur l'origine des cellules génitales primordiales chez les Urodèles.

Chez *Triton taeniatus* et *Amblystoma mexicanum* le plasme, se trouvant au pôle végétatif de l'oeuf indivisé, fournit au stade du bourgeon caudal la partie ventro-caudale de l'entoderme. Pendant le développement les déplacements de ce plasme présentent une analogie frappante avec le déplacement du „cytoplasme germinal" chez les Anoures, lequel fournit les cellules génitales (BOUNOURE). Cela a été constaté au moyen de marques colorées.

L'enlèvement de ce matériel chez les deux Urodèles au stade de la jeune gastrula ou au stade de l'œuf indivisé ne change pas le nombre des cellules génitales. (Série A.)

La partie dorsale de l'entoderme, particulièrement la couche, qui revêtit au stade du bourgeon caudal la cavité archentérique, provient de la couche superficielle de la partie ventrale du territoire végétatif de la jeune gastrula.

L'enlèvement de cette couche au stade de jeune gastrula produit une diminution considérable du nombre des cellules génitales. (Serie B). Chez les Urodèles cette partie du territoire végétatif joue un grand rôle dans la formation des cellules génitales. Cependant ceci ne démontre pas que les cellules génitales se forment par une différenciation de ce matériel indépendammant des tissus environnants. Une influence inductrice, provenant de ce matériel et agissant sur le mésoderme, ou une induction en sens invers, doit être considéré. Sous l'influence de cette induction les cellules génitales pourraient se former.

J'ai enlevé chez *Triton taeniatus* tout l'entoderme de la jeune

neurula, et j'ai pu constater que les animaux contenaient encore des cellules génitales. Cela porte à croire qu'un déplacement très précoce des cellules génitales de l'entoderme au mésoderme a eu lieu ici.

En 1939 dans les expériences de la série A, j'ai probablement enlevé chez quelques animaux en même temps le matériel de la serie B, ce qui alors a causé une reduction des cellules génitales (Séance du 20 avril 1940, Comptes Rendus de la Soc. Néerl. de Zoologie).

2. L. H. BRETSCHNEIDER (Utrecht). Die Oogenese von *Limnaea stagnalis* (L.).

Im Anschluss an die experimentelle Untersuchung an *Limnaea*-eiern (CHR. P. RAVEN, The effect of centrifugal force upon the eggs of *Limnaea stagnalis*. Comptes rend. néerl. zool. 1940), die ausgeht vom reifen, befruchteten Ei, interessierte uns die Frage, wie das Ei sich im Laufe der Oogenese bildet. Im reifen Ei konnten bisher verschiedene Bestandteile histo-chemisch nachgewiesen werden (Kern, hyalines Grundplasma, Eiweissdotter, Fett, Glutathion, Oxydase-Peroxydase, Pigment, bestimmte Granula und Vacuolen). Überdies besitzt das reife Ei einen einigermassen polären Bau indem in der animalen Eihälfte vorwiegend Plasma und der Kern, im vegetativen Teil der Dotter liegt. Das reife Ei kennzeichnet sich also bereits durch einen ziemlich komplizierten Bau. In welcher Form und zu welchem Zeitpunkte in der Oogenese alle diese Bestandteile auftreten, war die Fragestellung dieser Untersuchung. Über Entstehen, Vermehren und Verteilung von: Eiweissdotter, Fett, und Enzymen wurde bereits an anderer Stelle berichtet (L. H. BRETSCHNEIDER, Handelingen v. h. 28. Ned. Natuur- en Geneeskundig Congres, 1941).

Wir können hier hinzufügen, dass sich thymo-nukleinsaure Eiweisse nur in den Chromosomen der Oogonien und dann erst im reifen Ei zur Zeit der Reifungsteilung vorfinden, während sie im Gesamtverlaufe der Oocytenentwicklung fehlen. Die Polarität wird, bereits in der Gonade festgelegt. Während des Wachstums orientiert sich die Eiachse immer senkrecht zur Gonadenwand, wobei basal der vegetative Pol, lumenwärts der animale Pol liegt. Der Kern verschiebt sich schon sehr frühe gegen den animalen Pol. Aus der Zu- und Abnahme der Kerngrösse während der Oocytenentwicklung, der regen Stoffwechseltätigkeit des Nucleolus (Granula und Vacuolenbildung) und dem Auftreten und Verschwinden zahlreicher Granula (von

verschiedenem spec. Gewichte) im Kern, wird auf eine intensive Stoffwechselbeziehung zwischen Kern und Plasma geschlossen. Zentrifugieren der Gonade hat eine Stratifikation des Eiinhaltes zur Folge. Der aus Golgikörpern und Eiweisskristallen entstehende Dotter liegt im zentrifugalen Eiteil, die zu einer Fettkappe vereinigten Fettvacuolen und der Kern liegen zentripetal, während sich zwischen beiden eine Plasmazone befindet, in welcher sich flüssigkeitserfüllte Vacuolen und Vacuolen mit einem zentralliegenden Granulum befinden. Die Zentrifugalkraft stratifiziert auch den Kerninhalt, indem der schwere grosse Nucleolus zentrifugal orientiert ist und in einer Aussackung der Kernmembrane oder im Eiplasma liegt, während im Kernsaft, ihrem spec. Gewicht gemäss angeordnet, zalreiche Granula liegen. Aus der linearen Anordnung dieser Granula ist auf ein sie verbindendes Liningerüst zu schliessen.

3. N. TINBERGEN (Leyde). Sur le comportement de *Satyrus semele* (L.).

Séance du 19 décembre 1941 à Utrecht

1. H. J. JORDAN (Utrecht) donna un aperçu de ses recherches en collaboration avec M. N. Postma sur la régulation du tonus musculaire par les ganglions pédaux de *Helix pomatia* L.

On savait que les ganglions pédaux de l'escargot règlent la résistance contre une déformation passive des muscles selon leur propre état d'activité. Cet état d'activité s'accord avec la mesure de la déformation, à laquelle on a soumis les muscles du pied isolé de l'escargot. La réaction du muscle à cette régulation peut être l'augmentation ou la diminution de la résistance, dont il est question. Notre tâche a été, de localiser cette double influence de la part des ganglions. On n'avait pas réussi à atteindre ce but en changeant l'activité des ganglions par application de chloride de soude ou de cocaïne, à cause de la diffusibilité de ces substances. Nous avons remplacé ces moyens par des électrodes en contact avec un accumulateur, fournissant un courant d'un voltage insuffisant pour stimuler les muscles, mais assez fort pour provoquer un électrotonus. Le cathélectrotonus dorsal des ganglions active un centre excitateur, tandis que le cathélectrotonus ventral des ganglions augmente l'activité d'un centre inhibiteur du tonus musculair. Voir pour les détails Proc. Nederl. Akad. v. Wetensch., Vol. XLIV, p. 1169, 1941.

2. P. Triebels (Utrecht). Über einen Sperrmechanismus bei *Galeopterus.*

Galeopterus (*Galeopithecus*) *temminckii* ist ein baumlebendes Säugetier, das sowohl beim Klettern als beim Ruhen an den Krallen hängt. Die dafür notwendige dauernde Beugung der Krallen wird ohne Muskelwirkung durch einen Sperrmechanismus erhalten. An den ersten Phalangen der Finger und Zehen befinden sich in den Sehnenscheiden röhrenförmige, an der Innenseite quergerippte Ligamente. Die Sehnen der am Krallenglied inserierenden langen Beugemuskeln tragen an der Stelle, wo sie durch das Ligament gehen, knorpelige Zähne. Beim Hängen werden die Sehnen gegen die Wand der Sehnenscheide gezogen, sodass die Zähne ineinandergreifen; die Sehne wird gesperrt und die Kralle bleibt gebogen.

Dieselben Sehnen werden auch noch auf andere Weise fixiert; denn an der Stelle, wo sie über das Metacarpophalangealgelenk schleifen, sind sie verbreitert und knorpelig und werden dort von einer Schlinge umfasst, die aus den verwachsenen Sehnen des Musculus palmaris longus und M. flexor digitorum sublimis entsteht (beim Fuss aus der Aponeurosis plantaris und M. flexor digit. brevis).

Bei der Hand und dem Fuss ist die erste Phalanx rechtwinklig dorsal gebogen, die zweite und dritte stehen wieder parallel zur Mittelhand- und Mittelfussebene. Durch diese eigentümliche Stellung wirken sich beide Mechanismen beim Hängen an den Krallen maximal aus, denn dadurch wird die Sehne fest gegen die Scheide gezogen und die Aponeurose straffgehalten.

Beim Faultier *Choloepus didactylis* werden die Sperrschneiden der Hülse in die glatte elastische Sehnenoberfläche eingepresst.

Schaffer, der die Sperrvorrichtungen bei den Fledermäusen beschrieben hat, untersuchte auch *Sciurus* und fand dort merkwürdige Gelenke. Genau dasselbe findet sich auch bei den fliegenden Eichhörnchen *Sciuropterus* und *Pteromys*. Auch bei diesen Tieren nehmen die Knorpelzellen in den Fingergelenken nach der Gelenkoberfläche hin an Grösse zu und springen halbkugelförmig in die Gelenkhöhle vor. Die Funktion ist vielleicht diese, dass hierdurch bei den grossen Sprüngen der Stoss gedämpft wird.

3. J. Verwey (Leyde). Sur la périodicité annuelle dans la salinité de l'eau et la migration des animaux marins.

4. E. J. Slijper (Utrecht). Biologic-anatomical investigations on the bipedal gait and upright posture in mammals, with special reference to a little goat, born without forelegs.

Researches were made upon the characteristics of the locomotor apparatus in bipedal and upright going mammals. In the first place these researches concerned the structure of some parts of the skeleton (hindleg, pelvis, thorax, vertebral column) in running, walking, climbing, bipedal jumping and hanging-climbing mammals as well as in flying mammals and man. In the second place researches were made upon the skeleton and the musculature of a little goat, born without forelegs. This animal died at the age of one year. The first seven months of this year it passed its days on the grass-field, moving forward by jumps on the hind legs in a semi-upright posture. The manner of locomotion was quite similar to that of a kangaroo.

Characteristic adaptations to the bipedal gait and upright posture are:

1. *Pelvis.* a. The combination of a nearly vertical ilium with a very narrow angulus ilio-lumbalis. b. A widening of the lumbo-sacral angle in those bipedal mammals in which it is required by the capacity of the pelvic cavity. c. A lengthening of the ilium, almost exclusively caused by a lengthening of its presacral part (m. glutaeus med.). d. Lengthening of the ischium. e. Lengthening of the symphysis. f. Widening of the whole pelvis. g. Better development of the psoas musculature in bipedal jumping, minor development of these muscles in hanging-climbing mammals and man. The characteristics mentioned sub a, b, d, e and g were present in the bipedal goat in a very striking way. There was no lengthening of the ilium, since the lengthening of the fibres of the m. glutaeus medius was brought about by an elongation and better development of the gluteal tongue. The pelvis was very narrow at the acetabulum in order to bring the acetabular joint-surface in the same paramedian plane with the ilio-sacral joint (elimination of a part of the exorotation). Moreover all the bones of the pelvis were thickened to a very marked extent.

2. *Thorax.* a. Broadening and widening of the apertura thoracis and the cranial part of the thorax, broadening of the first

sternebra. b. Curvature of the proximal parts of the ribs in a dorsal direction. c. Broadening and widening of the whole thorax (barrel-shaped thorax). d. Broadening and shortening of the whole sternum; synostosis of the different sternebrae. All the above-mentioned characteristics were found in the bipedal goat to a more or less extent. Moreover, this goat showed a reduction of the number of lobes of the right lung. In mammals a reduction of the number of lobes of the lungs is often attended with a widening and broadening of the thoracic cavity.

See also: Proc. Nederl. Akad. v. Wetensch. **45**, 1942, p. 288; 407.

Séance du 24 janvier 1942 à Amsterdam

CHR. P. RAVEN (Utrecht). The neural crest.

The neural crest or ganglion crest is a peculiar structure in the development of the Vertebrates. Originating so early in development that it may be considered as one of the "primary organ rudiments", it has as such a temporary existence, as its material at an early stage is dispersed through the body, where its cells differentiate into various tissues. It does not wonder, therefore, that the neural crest from the time of its discovery has been the object of much controversy, and that we have only in the last years obtained a better insight in its development.

HIS described in 1868 the origin of the cranial and spinal ganglia of the chick from a strip of thickened ectoderm along the margin of the neural plate, called „Zwischenstrang" by him. According to BALFOUR (1877), these ganglia originate in the Selachii by proliferation from the roof of the neural tube after its closure. Since then, the development of the neural crest has been studied by many authors in various Vertebrates; its origin either from the neural tube or from the thin ectoderm outside the neural plate has been described many times; however, a generally accepted opinion as to its origin has not been attained. In the axolotl (*Amblystoma mexicanum*), it can easily be demonstrated that the material of the neural crest originates from a band of ectoderm, which surrounds the anlage of the central nervous system, and is lying at the open neural plate stage precisely at the limit between the thin ectoderm and the thickened epithelium of the neural plate. This band surrounds the neural plate also rostrally, so that the neural crest at a later stage reaches through the fore brain region anteriorly, as is confirmed by recent observations of BAKER & GRAVES. A study of the literature shows that the statements about the origin of the neural crest in other Vertebrates nearly always show an identical position of its material in the neurula.

During further development the cells of the neural crest in the head region of the axolotl move from their original dorsal position in a ventral direction along the sides of the head and penetrate into the visceral arches. This "mesectoderm" forms a part of the cranial ganglia; moreover, it furnishes mesenchyme in the ventral region of the head, from which the anterior parts of the cranial trabeculae and the cartilaginous visceral skeleton, with the exception of the posterior basibranchium, develop. From many observations of other authors it is apparent that the same happens in other Vertebrates; however, the origin of a part of the cartilaginous cranium from the "mesectoderm" could not yet be demonstrated in Sauropsids and Mammals.

The development of the neural crest in the trunk region of the Urodeles cannot be studied as easily. Experiments, in which a part of the primordium of this material was transplanted xenoplastically from the axolotl upon *Triton taeniatus*, showed, however, that the cells of the trunk neural crest move in 3 directions: ventrally between neural tube and somites; ventrolaterally between somites and epidermis, and dorsally into the dorsal fin. This is confirmed by recent observations of DETWILER (1937) by means of vital staining.

The differentiation of the material of the neural crest after its dispersion through the body can be studied by means of special experiments only. Much light was thrown upon it by the above-named experiment with xenoplastic transplantation of the trunk neural crest from axolotl to *Triton*, followed by measuring of the nuclei and statistical treatment of the results. These and other experiments showed that the material of the neural crest differentiates into the following tissue elements: ganglion cells of the cranial and spinal ganglia, sympathetic ganglion cells, cartilage of the head skeleton, connective tissue in head and trunk, expecially in the dorsal fin, in the corium, and the endomeninx, finally pigment cells.

The spinal ganglion cells come only from the neural crest. The same holds true for the transient ganglion cells of ROHON & BEARD, situated in the dorsal part of the neural tube in lower Vertebrates. The cranial ganglia, on the contrary, derive for a major part from ectodermal placodes on the sides of the head, whereas the neural crest furnishes only a minor portion of these ganglia. The sympathetic ganglion cells of the vertebral sympathetic ganglia have a double origin, coming partly from the neural crest, partly from the ventral half of the neural tube, as is shown by experiments, in which the median part of the neural plate was transplanted xenoplastically between axolotl and *Triton*. In this way, an old controversy as to the origin of these cells ends in a compromise. Experiments of HARRISON (1904) seemed to show that the sheath cells of SCHWANN derive from the neural crest, too. The xenoplastic transplantations showed, however, that this is not the case; these cells come, on the contrary, from the ventral part of the neural tube. This opinion is, however, not shared by most authors.

The development of a part of the cartilaginous cranium from cells of neural crest origin, as observed in sections of normal embryos, was confirmed in the following experiments: exstirpation of the neural crest, followed by defects in the head skeleton; heteroplastic orthotopic transplantation of this material, whereafter the cells retain their own specific growth rate, leading to disharmonies in the composition of the cranium (HARRISON); heterotopic transplantation of the cranial neural crest, differentiating into cartilage in the abdominal wall of the host, and retaining its species character after xenoplastic transplantation. The fact that the neural crest in the trunk region does not contribute to the development of the axial skeleton is rather remarkable.

In head and trunk, the neural crest forms large masses of connective tissue. Transplants from the neural folds nearly always form connective tissue, too. The development of the dorsal fin and, partly, of the gills is dependent upon the presence of this tissue. In Urodeles, it furnishes the material of the corium, as well as that of the endomeninx, whereas the ectomeninx derives at least in a large measure from mesenchyme of sclerotome origin. In the head, the tooth papillae and the osteoblasts, which form the bony skull, originate, in all probability, at least partly from the mesectoderm.

Finally, the neural crest forms many pigment cells. Experiments of DUSHANE prove, that in the Urodeles the melanophores, xanthophores and guanophores in the skin and the viscera (with the exception, perhaps, of the epidermal melanophores) derive from the neural crest. In the pigment formation of the subepidermal melanophores the overlying epidermis plays a part, as is shown in xenoplastic transplantation experiments with the white axolotl. In other Vertebrates, too, the neural crest furnishes pigment cells (DORRIS). Experiments of TWITTY with *Triturus* prove, that the species-specific character of the skin pigmentation depends upon the properties of these pigment cells of neural crest origin.

In view of the peculiar development of the neural crest, many problems as to the causality of this development arise. Experiments, in which the material of the neural crest was transplanted in early stages of development showed that in the Amphibia the tendencies for differentiation into cartilage, ganglion cells and connective tissue arise in a late gastrula stage. It is not yet known, however, what determines this material; probably, the lateral parts of the archenteron roof play a part in this determination process. We know that the neural crest may be induced independently from the central nervous system. What factors may be responsible for the extensive migrations of these cells, is not clear; an experimental investigation of this problem has begun. As to the inductive properties of the neural crest material itself, transplantations of *Rana* mesectoderm into *Triton* have shown that this material has an influence upon the determination of the neural plate and of the balancer of the host. Experiments of other authors prove the part the neural crest plays in the determination of the auditory vesicle (TRAMPUSCH), of the adhesive discs of Anura (VINTEMBERGER) and of the dorsal fin of the Urodeles (TERNI).

Séance du 21 mars 1942 à Utrecht

1. J. J. DUYVENÉ DE WIT (Utrecht) (en collaboration avec M. F. C. VAN DER KAAY et M. L. H. BRETSCHNEIDER): Relations entre le poids la grandeur des cellules théca et granulosa, la teneur en progesterone et lipoides du corps jaune de la vache pleine et la durée de la gestation.
   Voir: L. H. BRETSCHNEIDER, J. J. DUYVENÉ DE WIT und F. C. VAN DER KAAY: Die Beziehung zwischen Gewicht, Grösse der Theka- und Granulosazellen, Progesteron- und Fettgehalt des Corpus luteum graviditatis des Rindes und Schwangerschaftsdauer. Klin. Wchschr. 1942. p. 456.
2. V. WESTHOFF (Utrecht). La distribution des fourmis, leur position sociologique et l'écologie de leurs nids dans les forêts néerlandaises.

Pendant l'année 1941 nous avons fait des recherches sur la distribution quantitative des fourmis dans les forêts néerlandaises. Premièrement nous avons voulu contribuer à l'étude des biocoenoses en totalité (donc pas de la faune à part); de l'autre côté nous avons tâché d'être utiles à l'économie forestière, quelques espèces de fourmis étant utiles, d'autres nuisibles. Pour analyser des biotopes nous nous sommes servis de la méthode phytosociologique de BRAUN-BLANQUET, qui permet de les caractériser le plus exactement. Dans 8 des 11 provinces nous étudions 25 types de bois (14 associations et sous-associations, donc des forêts plus ou moins naturelles, et 11 types de bois culturels). Dans tous ces bois des relevés phytosociologiques (c'est-à-dire des recherches sur des surfaces déterminées, où sont notées toutes les espèces de plantes, leur abondance et leur dominance en chiffres, et les conditions écologiques) ont été faits sur 126 surfaces en total, chacune de 100 m²; le nombre des nids de fourmis de chaque espèce y fut déterminé; ensuite l'art de bâtir les nids et la conduite des fourmis y furent étudiés. C'est ainsi que nous avons fait des recherches sur 2000 nids environ; 23 des 48 espèces indigènes peuvent vivre dans les bois. Nous avons trouvés que chaque type de bois correspond à un ensemble spécial des fourmis. Le milieu le plus favorable est la forêt de chênes et de bouleaux (Querceto roboris-Betuletum typicum) du sol sec et silicieux: 16 espèces en total, nombre des nids sur 100 m² 17-82. L'étude du développement des plantations primitivement nues a indiqué, que l'étage herbacée décide en premier lieu de l'installation des fourmis et non pas la strate arborescente. A mesure que, par exemple, un bois de pins sylvestres s'enrichit d'un sous-bois et se développe pour devenir le climax, le nombre des espèces de fourmis augmente de 1 à 12, le nombre des nids de 3 à 78 sur 100 m².

Des faits intéressants faunistiques et écologiques furent constatés aussi. Comme les fourmis montrent une grande souplesse quant à l'art de bâtir leurs nids, l'étude des nids différents possibles dans les biotopes divers nous a donné une bonne idée de l'influence du milieu sur l'espèce.

Séance du 18 avril 1942 à Amsterdam

1. Mlle W. S. S. VAN BENTHEM JUTTING (Amsterdam). Mollusques d'eau douce de la partie sèche du nord-est du Brésil. Paraîtra dans: Archiv für Hydrobiologie.

2. H. Engel (Amsterdam). Sur le genre *Dolabella*.

D. gigas (Rang) seule se distingue par la coquille et le pénis armé, toutes les autres Dolabelles doivent être réunies dans une seule espèce *D. scapula* (Martyn), habitant l'Indopacific, de la Mer Rouge et l'Afrique du Sud, jusqu'aux côtes occidentales de l'Amérique.

Voir: Zoologische Mededeelingen, Rijksmuseum Nat. Historie, Leiden, XXIV, 1942, p. 197–239.

3. A. Punt (Utrecht). Problems in gas-exchange of fishes.

In addition to the publication by J. Jongbloed and A. Punt (Acta brevia neerlandica XII, 43, 1942) which described a new method of continuous determination of the "basal" gas-exchange in fish, the difficulties in measuring this value were discussed. The influence was shown of temperature, feeding, salt concentration and oxygen pressure. The correlation between gas-exchange and body weight and the surface-area law were discussed.

Séance du 21 mai 1942 à Groningen

J. Verwey (Leyde). La cause de la distribution de quelques Acéphales de la côte néerlandaise.

Séance du 3 juin 1942 à Amsterdam

B. J. Krijgsman (Utrecht). Une causerie générale sur les phénomènes électriques des nerfs et des muscles.

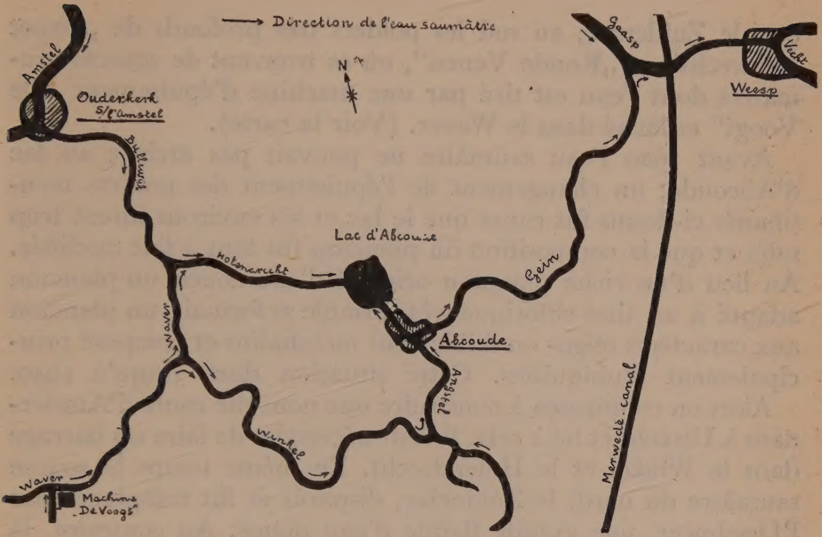
Séance du 12 juin 1942 à Utrecht

N. Tinbergen (Leiden). Une causerie générale sur les recherches éthologiques, spécialement dans la station zoologique du Helder.

Séance du 11 juillet 1942 à Abcoude, à la fin du cours de limnologie lacustre (du 23 juin au 11 juillet 1942 à Abcoude et encore du 13 au 27 juillet 1942)

1. A. van der Werff (Abcoude). Hydrographie et hydrobiologie du lac d'Abcoude.

Le lac d'Abcoude, situé au nord-ouest du village d'Abcoude (province d'Utrecht) est une flaque d'eau d'une profondeur maximale de 2.70 m., qui doit être considéré comme dilatation locale du système de cours d'eau, formé entre les deux vieilles branches du Rhin, les fleuves Vecht et Amstel.



Tous ces cours d'eau forment une partie du système de canaux, administré par le Conseil d'administration d'Amstelland et aussi le lac d'Abcoude en forme une subdivision.

A l'ouest le lac d'Abcoude se joint à l'Amstel par deux cours d'eau différents Angstel–Winkel–Waver et Holendrecht–Bullewijk; à l'est les petites rivières Gein et Gaasp forment la jonction avec le Vecht.

Par suite de l'écoulement de l'eau des polders dans le système des canaux et de ceux-ci dans l'IJsselmeer, l'eau du lac d'Abcoude présente une composition très variable. Cela fût déjà constaté en 1924, lorsque Mme. Wibaut-Isebree Moens, M. Heymann et M. Redeke firent des recherches détaillées sur l'hydrodynamie et les changements dans la composition de l'eau de cette région.

Des observations spéciales, faites simultanément à environ 80 stations, ont montré, qu'un courant saumâtre venait du nord par les rivières Amstel, Bullewijk et Holendrecht et un autre du sud par le Waver, Winkel et Angstel et plus dircetement encore par le Waver et Holendrecht.

Évidemment ces deux sources saumâtres donnèrent lieu à des variations considérables de la salinité de l'eau du lac d'Abcoude (Cl en mgr/l 66-1070).

On pouvait constater que la source saumâtre au nord devait être le Zuiderzee, au sud les polders très profonds de „Groot Mijdrecht” et „Ronde Venen”, où se trouvent de sources saumâtres dont l’eau est tiré par une machine d’épuisement „De Voogt” et lâché dans le Waver. (Voir la carte).

Avant 1920 l’eau saumâtre ne pouvait pas arriver au lac d’Abcoude; un changement de l’épuisement des polders mentionnés ci-dessus fût cause que le lac et ses environs furent trop salés et que la composition du plancton fût tout à fait modifiée. Au lieu d’un riche plancton originel d’eau douce, un plancton adapté à un titre chlorique très variable se formait, un plancton aux caractères oligo- ou faiblement mesohalins et composé principalement d’ubiquistes. Cette situation dura jusqu’à 1940. Alors on commença à construire une nouvelle route d’Amsterdam à Utrecht et lié à cela, il était nécessaire de faire un barrage dans le Winkel et le Holendrecht. En même temps la source saumâtre du nord, le Zuiderzee, disparût et fût remplacée par l’IJsselmeer, une grande flaque d’eau douce. Au contraire, la source saumâtre au sud existait toujours, mais pour le moment l’eau saumâtre du Waver ne peut pas arriver au lac d’Abcoude grâce aux barrages.

Actuellement le titre chlorique du lac est de 80 à 90 mgr/l. Cette situation dure déjà environ deux ans et continuera encore olngtemps. Des recherches nouvelles nous apprendront les modifications eventuelles du plancton et aussi, de quel genre elles seront.

2. B. J. KRIJGSMAN prononça, pour célébrer l’installation des cours de limnologie annuels à Abcoude un petit discours très spirituel sur: „Une nouvelle espèce du lac d’Abcoude”, qui a eu beaucoup de succès.